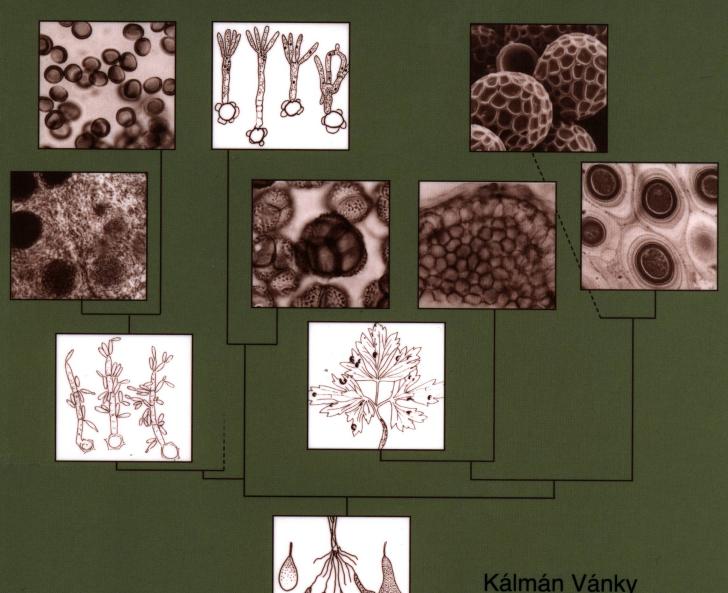
Illustrated Genera of Smut Fungi



Kálmán Vánky

Illustrated Genera of Smut Fungi

THIRD EDITION

Kálmán Vánky



The American Phytopathological Society St. Paul, Minnesota

Cover:

1st row:

Entorrhiza cypericola Fig. 21A.

2nd row:

Moesziomyces bullatus Fig. 54J. Entyloma microsporum Fig. 22A.

3rd row:

Langdonia fraseriana Fig. 44B. Thecaphora seminis-convolvuli Fig. 83B. Doassansia alismatis Fig. 17B. Georgefischeria riveae Fig. 37D.

4th row:

Ustilago hordei Fig. 97B. Urocystis occulta Fig. 94D. Tilletia caries Fig. 84B.

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PREFACE to the 1st edition

Smuts (Ustilaginales) and rusts (Uredinales) are two groups of basidiomycetous fungi parasitic on higher plants. These groups have much in common and are often compared with each other. The rusts constitute the larger group and are known to be of immense economic importance due to the serious losses they cause to numerous crop plants. Thus it is only natural that they have been intensely studied by numerous mycologists and plant pathologists.

But the role of the smuts in Nature must not be underrated. Their number of species is four-figured, and many cause considerable losses to cultivated plants. Nevertheless, the number of students has been much smaller; they are decidedly less known, and the literature about them is much more restricted.

They are, however, for the present intensely studied, and one of the most active workers is Dr. K. Vánky, who for three decades has devoted most of his time to the study of their taxonomy. Through world-wide travels and the performance of autopsies he became acquainted with more of them in the living state than any other mycologist. A leading theme in his studies has consistently been the generic level. He has been searching for new and more fundamental characteristics in order to get the genera, as far as possible, homogenous and phylogenetically coherent; he finds it now appropriate to publish the present guide to the acceptable genera (about 50 in number) and to discuss the remaining problems.

The aim of his treatise is purely practical, and so the smuts are taken in traditional sense, and those strange yeast-like saprophytes with similar spore germination are left out of account.

Each genus is given a brief concise diagnosis, which is "materialised" by a detailed, profusely illustrated description of its type species, which, as far as possible, is based on the type specimen or other authentic material. His most accurate and detailed drawings of infected plants reveal him as a highly gifted artist and the excellent microphotos (LM and SEM) testify his skills as a photographer.

This guide will certainly facilitate all future studies of the smuts and attract the attention of all those interested in morphological, ontogenetic and taxonomic mycology.

John Axel Nannfeldt

Professor emeritus in taxonomical botany

Jan axel Nannfeer J

University of Uppsala (Sweden)

Uppsala, May 23, 1985

PREFACE to the 2nd edition

Scientific work on smut fungi started in 1755 with the inspired field experiments of Tillet followed half a century later by Prévost's study, outstanding for its time, of germination of the spores of *Tilletia*. Much later in the latter half of the nineteenth century smut fungi attracted the attention of those giants of Mycology the Tulasne brothers, de Bary and especially Brefeld. They laid the foundations for work on Ustilaginales. In the late eighteen-eighties and well into the twentieth century research on the smut fungi centered around sex and nuclear behaviour, and taxonomy became rather unfashionable. Nevertheless Plowright, Zundel, Liro, McAlpine, Fischer and others made very valuable contributions in the form of regional smut floras.

During several decades at the end of last century and on-going, taxonomic studies on Ustilaginales have been dominated by the contribution of Kálmán Vánky. In numerous papers and in his encyclopaedic 'European Smut Fungi' he has described individual species, many new, illustrated by line drawings of infected plants and SEM photographs of spores. His pictures of plants attacked by smuts are not only informative but also of extreme delicacy and often beauty. He has collected all over the world with a genius for spotting a smutted plant. On the basis of his field work he has, over many years, built up the famous 'Herbarium Ustilaginales Vánky'.

During his massive work on smut fungi, he has had cause to review generic concepts. In 1987, in his 'Illustrated Genera of Smut Fungi', nearly fifty genera were recognized. Now, with that number increased by around 50%, a new edition is greatly to be welcomed.

C. Terence Ingold Professor emeritus

University of London (England)

C. Terance Ingolo

Cholsey, November 19, 2000

PREFACE to the 3rd edition

Although it is only 11 years since publication of the 2nd edition of *Illustrated Genera of Smut Fungi* (2002), the 3rd edition sees the inclusion of an additional 28 genera (and removal of three genera, which are synonymised), an increase of almost one-third. In mere quarter of a century the recognised genera of smut fungi has more than doubled from 47 in 1987 (1st edition of *Illustrated Genera*) to 104 (2013, 3rd edition), along with a concomitant increase in the number of species. This remarkable increase reflects the rapid progress in taxonomy of smut fungi at the generic level. Such progress can be attributed to three factors: 1) the intensity of collecting activity and morphological studies carried out by Dr Kálmán Vánky over the past 4–5 decades; 2) rapid progress in understanding the ultrastructure of smut fungi; and 3) the adoption of molecular methods, which has led to a better classification and insight into the relationships of smut fungi. The future is unlikely to see a major increase in the number of new genera, partly because collecting activity is now sporadic and such activity is generally not supported by funding agencies, but largely because the multiphasic approach of traditional morphology, ultrastructural studies and phylogenetic analyses, related to host plant taxonomy, has led to more stability with better defined genera (see also McTaggart *et al.* 2012 a, b, c).

Traditionally, smut fungi were considered to be a taxonomically discrete group of fungi. However, such a viewpoint is no longer tenable with the recognition that the Microbotryales are more closely related to rust fungi than to other smut fungi and the recent discovery, based on ultrastructural morphology and molecular data, that two genera of smuts are actually ascomycetous rather than basidiomycetous. The 3rd edition of this book synthesises all of the new information on the taxonomy of smut fungi and provides a means to key out all genera. The book treats traditional smut fungi, but also includes a section on the ascomycetous genera and a few genera of uncertain affinity

The 3rd edition of *Illustrated Genera of Smut Fungi* is a fitting tribute to the tireless efforts that Dr Vánky has applied to collecting and study of smut fungi globally. This book, in addition to the *Smut Fungi of the World* (Vánky, 2011'2012') will be the base-line for studies of smut fungi at the generic and specific level for many years to come.

Eric H.C. McKenzie

Mycologist

Landcare Research, Auckland (New Zealand)

Auckland, January 15, 2013

ZH.C. Milline

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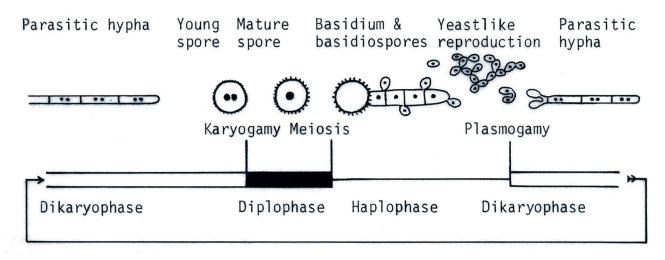
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INTRODUCTION

According to the classical concept, the smut fungi are plant parasitic basidiomycetous microfungi possessing teliospores. However, many species may have a shorter or longer saprobic phase to their life-cycle. Moreover, recent investigations show that the limits toward pure saprobic fungi are not as sharp as was thought earlier. There is even a pure saprobic smut fungus, *Tilletiaria*, known only from culture. Ultrastructural and molecular phylogenetic investigations have shown that there are groups of microfungi which do not have teliospores (e.g. Ceraceosorales, Malasseziales, Microstromatales, Exobasidiales) but they are closely related to the smut fungi and are classified under the Ustilaginomycotina. On the other hand, the Microbotryales, with teliospores and a life cycle similar to other smut fungi, are closely related to the rust fungi. In this book, smut fungus genera possessing teliospores, including the Microbotryales, are treated but plant and human pathogens which are lacking teliospores are omitted. The number of recognized smut fungus species in this sense is about 1700, distributed in 104 genera including two ascomyceteous genera. There are about 3500 synonyms to the species and c. 50 to the genera, including 10 anamorph genera. The species of host plants number approximately 4200.

The soma of the smut fungi consists of saprobic haploid cells and parasitic dikaryotic hyphae. In some species, the former are capable of prolonged yeast-like reproduction on nonliving substrates or also as hyphal anamorphs developed from basidiospores, capable of producing forcibly discharged ballistoconidia. The dikaryotic hyphae, with very few exceptions, are parasitic on angiosperms. The hyphae are septate, branched, usually intercellular, in some groups also intracellular, in some taxa forming haustoria in the host cells. In many cases hyphae are perennial within the host plant with little, if any evidence of their presence before spore formation begins. At spore formation karyogamy takes place and diploid spores are produced. The smut spores or teliospores (also called ustilospores, ustospores, chlamydospores, probasidia) are the organs of dispersion and of resistance. They are formed in the sori which consist of host tissues, of the spore mass, and in several genera also of modified fungal cells or tissues. The smut fungi produce a fascinating variation of symptoms on their hosts, developing sori of variable aspect in diverse organs: in the roots, stems, leaves, inflorescence, flowers, anthers, filaments, ovaries, etc. The spores may be single, in pairs, or aggregated in more or less persistent groups (spore balls). The spore balls may be composed entirely of fertile spores, or of a combination of fertile spores, sterile cells, and/or hyphae (comp. Vánky 1998e). At germination of the diploid spore, a basidium (also called promycelium, ustidium) is formed and meiosis takes place. The basidia give rise to haploid basidiospores (sporidia), or more rarely to haploid hyphae. These, or sometimes compatible basidial cells, fuse in pairs to restore the parasitic dikaryophase. However, there are many exceptions to this general scheme of nuclear phases (see Săvulescu 1957b:91-94). Several species within a few genera may possess anamorphs (conidial states). The infection may be localized, restricted to a certain organ or part of it, or generalized (systemic). Infected plants usually do not differ from healthy ones until the spores are formed.



General scheme of nuclear phases of the smut fungi.

THE CLASSIFICATION OF SMUT FUNGI

Since L.-R. & C. Tulasne (1847), the order Ustilaginales has generally been divided into two families, **Ustilaginaceae** and **Tilletiaceae**. The first is characterized by a septate (phragmo) basidium developing basidiospores laterally and terminally. The Tilletiaceae have a non-septate (holo) basidium with terminal basidiospores. Based on dissimilar types of basidia, some changes have been made to this system, such as the proposal of the family **Yeniaceae** Liou (1949), and the family **Glomosporiaceae** Ciferri (1963a). Another family, the **Graphiolaceae** Clem. & Shear, comprising some palm parasitic fungi, have been regarded as either imperfect fungi, doubtful smut fungi (e.g. Moesz 1950:222), or closely related to the smut fungi (Oberwinkler *et al.* 1982). Swann, Frieders & McLaughlin (1999:64) stated that "Multiple lines of evidence indicate that basidial characters are generally inappropriate for phylogenetic inference and, therefore for systematic consideration".

Earlier, the distinction between families was based exclusively on basidial characters, and that between the genera on characters of the sori, on spore- and spore ball formation and development, on presence or absence of sterile cells or other fungal elements within the spore balls or between them, and on spore germination. In species delimitation, the color, shape, size and ornamentation of the spores, spore balls and sterile cells, the structure of the spore balls, as well as host plant taxonomy were used (comp. Vánky 1991a; 2011('2012'). All these characters may vary considerably within the smut fungi which opens the way for subjectivism. The possibility of convergent evolution and evolutionary parallels for almost all characters mentioned above, complicated the situation even more.

The classical **morphological studies** of the sori, spore- (or spore ball-) development, mature spores and basidia did not provide adequate differentiating characters for the construction of a comprehensive classification on suprageneric level. Using molecular phylogenetic (Blanz & Gottschalk 1984, Gottschalk & Blanz 1985, Swann & Taylor 1995) and chemical methods (Deml, in Hoog *et. al.* 1987, Prillinger *et al.* 1990, 1991, 1993) surprising results were published, suggesting that the classification of the "smut fungi" is not as simple as was thought earlier and radical changes could be expected. Two new methods of study led to major changes in the fossilized, Tulasnean classification of smut fungi. The first one was the development of high-power transmission electron microscopes and modern methods of **ultrastructural studies**. The second one was the elaboration of **molecular phylogenetic** methods combined with computerized treatment of the obtained data. Using ultrastructural characters Bauer, Oberwinkler & Vánky (1997) proposed a new classification of the smut fungi and allied genera. This was improved and complemented by Begerow, Bauer & Oberwinkler (1998'(1997')), Piepenbring, Begerow & Oberwinkler (1999), Vánky (2001b), Bauer, Begerow, Nagler & Oberwinkler (2001), McTaggart, Shivas, Geering, Vánky & Scharaschkin (2012a, b, c), and summarized by Vánky (1999b) and Bauer *et al.*, in McLaughlin *et al.* (eds.; 2000).

This new classificatory system of smut fungi, based on ultrastructural and molecular phylogenetic studies, but also taking into consideration classical, morphological characters and host plant taxonomy, reflects more than ever before the phylogenetic relationship between these groups of fungi. The most surprising results of this new classification were:

- 1. The Microbotryales are more closely related to the rust fungi than to the smut fungi.
- 2. Some groups of fungi lacking teliospores (Malasseziales, Microstromatales, Exobasidiales) are closely related to the smut fungi.
- **3.** Through convergent evolution, similar, complex spore ball structures evolved from different ancestors as adaptation to parasitism on water plants (Doassansiopsidaceae and Doassansiaceae).
- **4.** The presence (or absence) of spore balls does not always reflect a close relationship e.g. although the Doassansiaceae is characterized by spore balls, *Doassinga* has single spores. Some monophyletic genera such as *Orphanomyces, Schizonella, Thecaphora* or *Ustanciosporium* contain species with single spores and species with spore balls.
- **5.** Some ancestors of the smut fungi jumped hosts to unrelated plants. All species of *Ustilago* (c. 200) are parasites on the monocotyledonous grasses (Poaceae). Back in evolutionary time, a species of *Ustilago* jumped from a monocotyledonous grass onto the dicotyledonous *Polygonum* (Weiss *et al.* 2004). The morphology of the sori and spores, as well as its dispersal strategy changed markedly during the time. Today, this smut is known as *Melanopsichium* (with 2 closely related species) on numerous *Polygonum* species.

6. Many morphologically identical and indistinguishable species of smut fungi, infecting the same host species, are in fact distinct species. These are called **cryptic species** and can only be revealed by molecular phylogenetic analyses. In dichotomous keys, based on morphological characteristics, they are twin species. One cryptic species is *Microbotryum chloranthae-verrucosum* M. Lutz, Göker, Piątek, Kemler, Begerow & Oberw. on *Silene chlorantha* (Willd.) Ehrh. (Caryophyllaceae; comp. Lutz et al, 2005). The cryptic twin of *M. chloranthae-verrucosum* is *M. violaceoverrucosum* (Brandenb. & Schwinn) Vánky. What's more, even a cryptic genus, *Salmacisia* D.H. Huff & A. Chandra was described which morphologically is indistinguishable from *Tilletia* Tul. & C. Tul.

Contrary to the cryptic species are the **pseudomorpho species**. A collection of *Antherospora vaillantii* (Tul. & C. Tul.) R. Bauer, M. Lutz, Begerow, Piątek & Vánky (syn. *Ustilago vaillantii* Tul. & C. Tul.) was discovered on *Muscari tenuiflorum* Tausch (Hyacinthaceae; comp. Bauer *et al.* 2008), in which the spores are considerably larger than in the type (instead of 6-11.5 µm they are 8-16.5 µm long). Despite this considerable morphological difference, DNA analysis did not reveal any difference between this and other collections of this species on the same host species.

Whereas the smut fungi are a phylogenetically heterogeneous group, there are fungi within the Ustilaginomycotina which are NOT smut fungi, because they do not produce teliospores. They are plant parasitic, more rarely saprobic, or human parasites. (Ceraceosorales, Microstromatales, Exobasidiales, Malasseziales). To this last order belongs *Malassezia furfur*, the causal agent of a common, superficial human skin disease, called tinea or pityriasis versicolor.

Some smut fungi may have an **anamorph** (conidial stage), and some smuts may grow in culture as yeast. Ultrastructural studies of basidiomycetous yeasts showed that their cell wall has a laminated structure and that bud scars are frayed. Begerow, Bauer & Boekhout (2000) published a comprehensive study of the "ustilaginomycetous anamorphs", based on nuclear LSU rDNA sequences, and integrated them into the new phylogenetic system of smut fungi.

Applying ultrastructural and DNA analyses on a large number of diverse species resulted in radical changes in the classification of smut fungi (see below). It became evident, that the term "smut fungus" is not a taxonomic term. Namely, the smut fungi are a phylogenetically heterogeneous group of microfungi having similar life strategy and organization (Bauer *et al.* 2000). In other words the smut fungi are plant parasites that develop teliospores as organs of dispersal and resistance. The results of the germination of teliospores are able to infect the host plants, to which the smut fungi are more or less strongly restricted. This definition can be applied to many basidiomycetous but also to some ascomycetous fungi (*Restilago, Schroeteria*) and maybe also to other groups of fungi (Vánky 2008b:97).

The number of smut fungi

Hawksworth (2001) estimated the number of the existing fungi on the earth to be 1.5 million, whereas the number of the known fungi is about 100000. This means that the 1700 recognized smut fungi represent 1.7 % of all the 100.000 known species of fungi. At the same time, the known smut fungi represent only roughly one third of the existing smut fungi, which I estimated to be in the range 4000- 4500 (Vánky, 2002c:169). The proportion of 1:3 of the known to the estimated upper limit of smut fungi is much higher than that of 1:15 for all fungi of the world (100000:1500000). The world-wide existing number of host plant species is a strongly delimiting factor for the number of species of plant parasitic fungi.

RESULTS AND PROBLEMS OF THE CLASSIFICATION OF SMUT FUNGI

Since publication of the 1st edition of the *Illustrated Genera of Smut Fungi* (Vánky 1987a), in which 47 (+8) genera were presented, and the 2nd edition (Vánky 2002a), in which 77 genera were recognized, many changes in the classification of the smut fungi have been made. Besides description of numerous new species, 28 new genera have been published, and the new classification system of the smut fungi and allied taxa has been elaborated. Many taxonomic and nomenclatural problems have been solved. However, the number of species investigated by modern methods (ultrastructure, molecular phylogeny) is still relatively small. As long as sequence data are not available for all known species of a certain group, a phylogenetically-based classification system will still undergo changes. As more taxa are added to comparisons, even major branches may change position. Investigations in this direction will certainly bring further changes.

Below, I have selected a few examples to present recent results or changes in the taxonomy of the smut fungi, and to highlight existing problems.

The Entorrhiza group

The species of *Entorrhiza* C.A. Weber represent a natural group, rather distant from other smut fungi. They are classified into their own class Entorrhizomycetes Begerow, M. Stoll & R. Bauer. The sori are produced on the roots of Cyperaceae and Juncaceae as small, often digitate galls in which the pale colored spores are produced intracellularly. Spore germination is also unique, with a four-celled basidium which remains inside the spores. Ultrastructurally the genus is characterized by dolipore septas without membranous plates or caps, intracellular hyphae with local interaction zones without interaction apparatus, and the presence of haustoria. At present 14 species of *Entorrhiza* are known but this number will certainly increase when further targeted searches are made for the genus.

Recently, another genus, *Talbotiomyces* Vánky, R. Bauer & Begerow (2007) was described, producing galls on the roots of dicotyledonous host plants (Aizoaceae, Molluginaceae, Portulacaceae) and intracellular, lightly pigmented spores. It has simple septal pores and haustoria. It is related to *Entorrhiza*, both probably at the base of the phylogeny of smut fungi or outside them.

The Urocystidales

The order Urocystidales R. Bauer & Oberw. is characterized by enlarged interaction zones, simple septal pores and presence of haustoria. It comprises 5 families and 12 genera: 1. Doassansiopsidaceae (Doassansiopsis), 2. Floromycetaceae (Antherospora, Floromyces), 3. Glomosporiaceae (Thecaphora), 4. Mycosyringaceae (Mycosyrinx) and 5. Urocystidaceae (Flamingomyces, Melanoxa, Melanustilospora, Mundkurella, Urocystis, Ustacystis, Vankya).

Doassansiopsis (Setch.) Dietel resembles members of the Doassansiaceae in morphology of the spore balls, color and morphology of the spores, spore germination and ecology of the fungi, but differs in its ultrastructure. Antherospora R. Bauer, M. Lutz, Begerow, Piatek & Vánky produces its sori in the flowers (mostly anthers) of plants in Hyacinthaceae. Floromyces Vánky, M. Lutz & R. Bauer produces sori in the flowers of Agavaceae, Flamingomyces R. Bauer, M. Lutz, Piątek, Vánky & Oberw. in the basal part of the leaves of Ruppiaceae, Melanoxa M. Lutz, Vánky & R. Bauer in vegetative parts of plants in Oxalidaceae. Melanustilospora Denchev has sori in the leaves of Araceae, and Mundkurella Thirum. in various organs of plants in Araliaceae. The genus Urocystis Rabenh. ex Fuckel comprises also Tuburcinia Fr. and Ginanniella Cif. It is characterized by spore balls consisting of one to several pigmented spores surrounded by sterile cells. Sterile cells may be only a few or even lacking in some balls or may form one, rarely two, well-developed layers. The presence or absence of an anamorph, as well as the number of spores and sterile cells in the spore balls served as characters for recognizing three separate genera (comp. Ulbrich 1940). Because of intermediate forms, only one genus, Urocystis, is recognized. It is a natural, morphologically well-characterized genus, despite the fact that the c. 170 known species of *Urocvstis* parasitize a wide range of host plants in 16 monocotyledonous and 15 dicotyledonous families. Ustacystis Zundel has sori in the leaves of Rosaceae. Species of Vankya Ershad occur in the leaves of Liliaceae.

Smut fungi on Poaceae: The Sporisorium - Ustilago group

About 860 species of smut fungi parasitize grasses. These smuts are variable and belong to 20 genera. Grass parasitizing species of "Cintractia", "Sorosporium", "Sphacelotheca", Sporisorium and Ustilago were often placed alternatively in one of these genera by different mycologists, depending on which characters or character complexes were emphasized in their classification (e.g., presence or absence of spore balls, sterile cells between the spores or spore balls, peridium around the sori, columella in the sori, color and consistency of the spore masses, etc.). Of these Sphacelotheca is restricted to hosts in the Polygonaceae, Sorosporium (= Thecaphora) to dicotyledonous host plants, Cintractia to Cyperaceae. Having excluded these genera, in addition to some smaller, well delimited grass-parasitizing genera such as Bambusiomyces, Eballistra, Franzpetrakia, Fulvisporium, Jamesdicksonia, Macalpinomyces, Moesziomyces, Phragmotaenium, Tolyposporella, Tubisorus, Tranzscheliella, Urocystis, Ustilentyloma and those of the Tilletia group (Conidiosporomyces, Ingoldiomyces, Neovossia, Oberwinkleria, Tilletia), two large grass parasitizing genera remain, Sporisorium and Ustilago.

Recent molecular phylogenetic analyses (Stoll, Begerow & Oberwinkler 2005) showed that the analyzed species of *Sporisorium* and *Ustilago* form four major groups: *Sporisorium* gr. 1, *Sporisorium* gr. 2, *Ustilago*, and a mixed group of *Ustilago* and *Sporisorium*. Several *Macalpinomyces* species belong also to these groups.

McTaggart et al. (2012c) divided the group into the following seven genera: Anthracocystis, Langdonia, Macalpinomyces, Sporisorium, Stollia, Triodiomyces and Ustilago.

Tolyposporium, Moreaua, Restiosporium and Heterotolyposporium

A common character for these genera are the darkly pigmented spores forming spore balls. The genus *Tolyposporium* was introduced by Woronin (1882 ('1881')) for *Sorosporium junci* J. Schröter. This species parasitizes *Juncus* species (Juncaceae), forming black, external, naked, tumor-like sori in the flowers and on the culms, composed of a granular-agglutinated mass of spore balls. Over the years, more than 40 species of fungi with spore balls and an uncertain systematic position have been included in this heterogeneous genus, including species with widely different morphology and biology (Vánky 1977). Several of these species actually are mitosporic fungi, others belong to *Entyloma*, *Fulvisporium*, *Macalpinomyces*, *Moesziomyces*, *Schizonella*, *Sporisorium*, *Thecaphora* or *Urocystis*. Two additional species are on members of Cyperaceae (*Isolepis*) but the great majority of "*Tolyposporium*" species on Cyperaceae belong to the genus *Moreaua* T.N. Liou & H.C. Cheng (38 species), and those on Restionaceae to the genus *Restiosporium* Vánky (21 spp.).

The presence of two kinds of spores in both known species of *Heterotolyposporium* is a unique feature within the smut fungi. Piepenbring, Begerow & Oberwinkler (1999:496), and Piepenbring & Begerow (in Piepenbring, 2000:329), relied on molecular similarities and ignored the presence of the second type of spores, the hyaline ones (which they called "sterile cells"), considered *Cintractia piluliformis* (*Heterotolyposporium piluliforme*) to be a member of the genus *Tolyposporium*.

Ultrastructurally, *Tolyposporium*, *Heterotolyposporium* and *Moreaua* have the characters both of the Ustilaginaceae and Anthracoideacea families (intracellular hyphae, enlarged interaction zones and poreless septa). However, based on molecular biological analyses and host plant criteria, *Tolyposporium*, *Heterotolyposporium* and *Moreaua* were placed into the Anthracoideaceae, *Restiosporium*, together with *Websdanea*, remained in the Websdaneaceae (Begerow, Stoll & Bauer 2007('2006')).

Anthracoidea, Cintractia and related genera

The genus *Anthracoidea* was introduced by Brefeld in 1895 to accommodate *A. caricis* (Pers.) Bref., a smut fungus which produces localized, floral infection and black sori in the utricles of *Carex pilulifera*, and spores which germinate by a two-celled basidium. This genus was long neglected, and all smuts with black sori on Cyperaceae and single spores were treated under the older name *Cintractia* Cornu (1883). The type, *Cintractia axicola*, however, has a four-celled basidium and produces localized infection, usually on the floral pedicels. Kukkonen (1963) reinstated the genus *Anthracoidea*. Closely related to the genus *Anthracoidea* is the unispecific *Planetella* Savile, in the utricles of *Carex maritima*, possessing spores with a dark, thickened equatorial band and light, thin-walled, polar areas. Spore germination is not known.

Anthracoidea, Cintractia and other related genera have in common the dark, black color of the spore masses, spores usually single, host plants in the Cyperaceae and/or Juncaceae, and ultrastructure consisting of intracellular hyphae, enlarged interaction zones and poreless septa. Based on this ultrastructure they were placed

into the Ustilaginaceae (Bauer et al. 2000). However, Begerow et al. (2007('2006')) used molecular analyses to demonstrate that species of Anthracoidea, Cintractia, Dermatosorus, Farysia, Heterotolyposporium, Moreaua, Planetella, Schizonella, Stegocintractia, Tolyposporium and Trichocintractia form a monophyletic clade. They consider that Ustilaginales parasitic on Cyperaceae and Juncaceae are best placed in the Anthracoideaceae Denchev.

Anthracoidea, with c. 100 known species, forms a natural group, parasitizing members of Cyperaceae: Carex, Carpha, Fuirena, Kobresia, Schoenus, Scirpus (Trichophorum), Uncinia. The taxonomy of the genus is difficult and in need of study by modern, molecular phylogenetic methods (comp. Hendrichs et al. 2005), combined with detailed morphological studies of the spores. The obtained results must be interpreted and evaluated on the basis of host plant taxonomy. Unfortunately, after the publication of the paper of Vánky (1979), there is a dangerous tendency to consider all morphologically slightly different collections on a certain section of Carex to be separate, good species, increasing unnecessarily the number of taxonomic synonyms. Anthracoidea species may occur not only on members of related sections but in some cases also on several, widely distant sections. A good evidence for such a wide host spectrum is the morphologically typical A. fischeri (P. Karsten) Kukkonen, with echinulate spores, occurring on members of the sections Divisae, Glareosae (Canescentes), Heleoglochin, Holarrhenae, Ovales, Stellulatae, Tenuiflorae and Vulpiae of the subgenus Vignea.

The heterogeneous *Cintractia* Cornu, s. lat. was studied by Piepenbring, Begerow & Oberwinkler (1999) and Piepenbring (2000), also using molecular data. The genus was split into four genera: *Cintractia* Cornu, s. str. (11 spp.) on Cyperaceae, *Leucocintractia* M. Piepenbr., Begerow & Oberw. (4) on Cyperaceae, *Stegocintractia* M. Piepenbr., Begerow & Oberw. (6) on Juncaceae, and *Gymnocintractia* M. Piepenbr., Begerow & Oberw. (*Eustanciosporium* Vánky; 20 spp.) on Cyperaceae. *Cintractia fimbristylidicola*, showing an isolated position on the molecular phylograms, was placed into the genus *Pilocintractia* Vánky (2 spp.) on Cyperaceae.

The Georgefischeriales

The order Georgefischeriales R. Bauer, Begerow & Oberw. is characterized ultrastructurally by poreless septa and small, local interaction zones without interaction apparatus. It contains four families and seven genera (comp. Bauer, Begerow, Nagler & Oberwinkler, 2001): Georgefischeriaceae (*Georgefischeria, Jamesdicksonia*), Tilletiariaceae (*Phragmotaenium, Tilletiaria, Tolyposporella*), Eballistraceae (*Eballistra*) and Gjaerumiaceae (*Gjaerumia*). The dark-spored "*Entyloma*" and "*Melanotaenium*" species on Poaceae and Cyperaceae belong to the Georgefischeriales. The problem is that knowledge of soral and spore morphology alone is insufficient to ascribe the numerous existing candidates for the Georgefischeriales to any of the taxa of this group. Spore germination or/and molecular data are necessary for that. The main differentiating characters of these genera are given in a key.

Key to the genera of Georgefischeriales

Spore germination results in phragmobasidia	2
— Spore germination results in holobasidia	4
2. Teliospores echinulate	tiaria
— Teliospores smooth	
3. Teliospores single	nium
— Teliospores in balls	
4. Ballistosporic propagules absent	
— Ballistosporic propagules present	5
5. On Convolvulaceae	heria
— Not on Convolvulaceae	6
6. On Poaceae and Cyperaceae	sonia
— On Liliaceae s. lat	umia

The Tilletia group

The sole family of the order Tilletiales Kreisel ex R. Bauer & Oberw., the Tilletiaceae Tul. & C. Tul., emend. R. Bauer & Oberw., is ultrastructurally characterized by intercellular hyphae and lack of an interaction

apparatus. The septal pore is a dolipore traversed by two membranous plates, pore caps are lacking. The following six genera belong here: *Conidiosporomyces* Vánky (3 spp.), *Ingoldiomyces* Vánky (1), *Neovossia* Körn. (1), *Oberwinkleria* Vánky & R. Bauer (1), *Salmacisia* D.R. Huff & A. Chandra (1) and *Tilletia* Tul. & C. Tul. (c. 180). All species of these genera are host plants in the Poaceae, with a few exceptions in the ovaries. The main differentiating characters of these genera are given in a key.

Key to the genera of the Tilletiaceae

1. Spores mixed with groups of Y-shaped, hyaline conidia	Conidiosporomyces
— Spores not mixed with groups of Y-shaped conidia	2
2. Spores elongate, foveolate, provided with a long, hyaline appendage	
— Spores globoid, not foveolate, not provided with a long, hyaline appendage	
3. Basidia reduced to the spores; spores with a dark, pigmented ring	
— Basidia not reduced to the spores; spores without a dark, pigmented ring	4
4. Basidiospores 1-2, ballistosporic; spores peculiarly ridged	Ingoldiomyces
— Basidiospores several, not ballistosporic; spores not peculiarly ridged (usually	
reticulate or verrucose, exceptionally smooth)	Tilletia / Salmacisia

The delimitation of these genera raises no particular difficulties. Several species of *Tilletia* weres often considered to belong to *Neovossia*. However, in considering *Neovossia* a unispecific genus, all the remaining species belong to *Tilletia* and one species to the cryptic genus *Salmacisia*.

"Tilletia" species on non-gramineous host plants do not belong to this genus, e.g., T. arctica Rostr. on Carex (Cyperaceae) is Orphanomyces arcticus (Rostr.) Savile, T. commelinae Kom. on Commelina (Commelinaceae) belongs to the genus Bauerago Vánky, T. euphorbiae Lenz on Euphorbia (Euphorbiaeae) is Melanotaenium euphorbiae (Lenz) M.D. Whitehead & Thirum., T. rhei Zundel on Rheum (Polygonaceae) is Microbotryum rhei (Zundel) Vánky, and T. thlaspeos Beck on Thlaspi (Brassicaceae) is Thecaphora thlaspeos (Beck) Vánky.

The Entylomatales

The order Entylomatales R. Bauer & Oberw. has only one family, Entylomataceae R. Bauer & Oberw., with one genus: *Entyloma* de Bary. It is characterized by single, pale colored spores embedded in the host tissue, and by spore germination with holobasidia. Ultrastructurally the simple septal pore with membrane caps, interaction apparatus with homogenous contents and lack of haustoria are typical. There are over 180 recognized *Entyloma* species, all on dicotyledonous host plants, belonging to 25 families. Most of the species occur on Asteraceae (86 species), followed by Apiaceae (17) and Ranunculaceae (11). "*Entyloma*" species on monocotyledonous host plants do not belong to this genus. Those on Poaceae possessing pale spores and phragmobasidia are *Ustilentyloma* (4 species) and, those possessing dark spores belong to the Georgefischeriales. Dark-spored "*Entyloma*" species on Cyperaceae (3 spp.) and Juncaceae (2 spp.) belong also to the Georgefischeriales. Some "*Entyloma*" species on Alismataceae are *Doassansia* species, those on Nymphaeaceae are *Rhamphospora*, on Sparganiaceae are *Nannfeldtiomyces*, on Callitrichaceae are *Doassinga* species, tree species on Liliaceae s. lat. belong to the genus *Gjaerumia*.

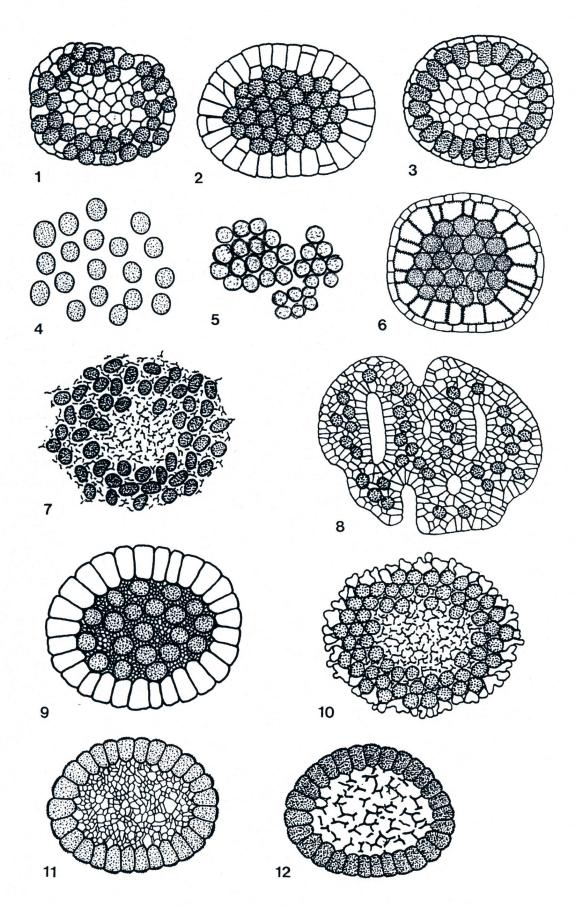
The Doassansia group

The "Doassansia" group contains 60 species, adapted to aquatic or paludal plants of widely different genera. These smut fungi produce pale colored spores agglutinated in spore balls which are embedded in the host tissues appearing as minute, brown dots within yellowish or brown leaf spots. The spore balls are composed of spores, sterile cells and/or hyphae in various arrangements. The arrangement of these components and the structure of the spore balls are used for their generic delimitation (Pl. I, pg. 17). Twelve genera have been recognized: Burrillia Setch. (4 spp.), Doassansia Cornu (12), Doassansiopsis (Setch.) Dietel (14), Doassinga Vánky, R. Bauer & Begerow (1), Entylomaster Vánky & R.G. Shivas (2), Heterodoassansia Vánky (8), Nannfeldtiomyces Vánky (2), Narasimhania Thirum. & Pavgi (1), Pseudodermatosorus Vánky (2), Pseudodoassansia (Setch.) Vánky (2), Pseudotracya Vánky (1) and Tracya H. & P. Sydow (2). Until recently, it was thought that the "Doassansia" group represents a morphologically, ecologically and phylogenetically natural group. However, ultrastructural studies (Bauer et al. 1997) and molecular analyses (Begerow et al. 1998('1997')) demonstrated

that the genus *Doassansiopsis* is not related to other genera of this group. This means that similar spore ball structures, adapted to aquatic or paludal plants and environment, developed from different ancestors by convergent evolution. In the new classificatory system *Doassansiopsis* belongs to the Doassansiopsidaceae, within the order Urocystidales of the subclass Ustilaginomycetidae. Ultrastructurally it is characterized by haustoria and a simple septal pore with two membrane caps and two non-membranous inner plates closing the pore. All other genera of the "*Doassansia*" group are classified into the Doassansiaceae, within the order Doassansiales of the subclass Exobasidiomycetidae. They are characterized by a complex interaction apparatus with cytoplasmic compartments, the absence of haustoria and by a simple septal pore with two membrane caps, without inner plates. Ultrastructural and molecular studies also demonstrated that not necessarily all members of the Doassansiaceae form spore balls, e.g., "*Entyloma*" *callitrichis* Liro, producing single spores in the leaves of the aquatic *Callitriche*, also belongs to the Doassansiaceae as *Doassinga*.

Key to the genera of Doassansiaceae and Doassansiopsidaceae 1. Spores single, not in balls	Doassinga
— Spores in loose or permanent spore balls	
2. Spore balls without cortex	
— Spore balls with cortex	
3. Spore balls friable, consisting of branched hyphae in which the spores are scattered	Nannfeldtiomyces
— Spore balls persistent, without branched hyphae	4
4. Spore balls consisting of parenchymatous sterile fungal tissue in which the spores are scat	
— Spore balls composed of spores only	Entylomaster
5. Cortex of firmly united spores	
— Cortex of sterile cells	7
6. Central part of the spore balls consisting of a network of branched hyphae	Tracya
— Central part of the spore balls consisting of a parenchymatous fungal tissue	Pseudotracya
7. Spore balls lobed and also containing cavities	Narasimhania
— Spore balls not lobed, compact, without cavities	
8. Central part of the spore balls composed of hyphae; spores situated between these and the	
— Central part of the spore balls not composed of hyphae	9
9. Central part of the spore balls composed only of parenchymatous sterile cells; spores	
situated between these and the cortex	_
— Central part of the spore balls composed of spores or also of sterile cells	
10.Central part of the spore balls composed of spores only	
— Central part of the spore balls composed of spores scattered in a network of sterile fungal of	
<i>P</i>	
11. Cortical cells of the same kind, not ornamented	Doassansia
— Cortical cells of two kinds: external, small, not ornamented, and internal, larger,	
ornamented on their inner surface	Heterodoassansia

Pl. I. Spore ball structure (and spores) of the genera 1. Burrillia Setch., 2. Doassansia Cornu, 3. Doassansiopsis (Setch.) Dietel, 4. Doassinga Vánky, R. Bauer & Begerow, 5. Entylomaster Vánky & R.G. Shivas, 6. Heterodoassansia Vánky, 7. Nannfeldtiomyces Vánky, 8. Narasimhania Thirum. & Pavgi, 9. Pseudodermatosorus Vánky, 10. Pseudodoassansia (Setch.) Vánky, 11. Pseudotracya Vánky, and 12. Tracya H. & P. Sydow (Drawings somewhat schematic).



The Microbotryales

The order Microbotryales, with 105 known species, is closely related to the rust fungi, possessing intercellular parasitic hyphae lacking interactions with deposits of specific fungal vesicles. Savile (1953:667) and Nannfeldt (in Lindeberg 1959:150) predicted that *Ustilago* species with violet tinted spores do not belong to that genus. These species all belong to the genera in the Microbotryaceae. Blanz & Gottschalk (1984), based on analyses of 5S rDNA, demonstrated that "smuts parasitizing dicots represent a group different from the graminicolous one". These results were confirmed by Prillinger *et al.* (1991, 1993) using biochemical methods. They analyzed, the neutral sugar pattern of the cell walls and found that dominance of mannose and presence of fucose is typical for the *Microbotryum* group. Following the molecular (18S rRNA) studies of Swann & Taylor (1995), the ultrastructural studies of Bauer *et al.* (1997), and the molecular (LSU rDNA) studies of Begerow *et al.* (1998('1997')), this group of fungi was placed under the subphylum Pucciniomycotina, class Microbotryomycetes, order Microbotryales, with two families, Microbotryaceae R.T. Moore, emend. R. Bauer & Oberw., and Ustilentylomataceae R. Bauer & Oberw. Both families comprise four genera: *Liroa, Microbotryum, Sphacelotheca* and *Zundeliomyces*, and *Aurantiosporium, Bauerago, Fulvisporium* and *Ustilentyloma*. For the detailed history see Vánky (1998c).

The genera *Bauhinus* R.T. Moore (1992:98) and *Haradaea* Denchev (in Denchev, Moore & Shin 2006:72) were subsequently segregated from *Microbotryum* sensu Vánky (1998c). *Bauhinus* was proposed for *Ustilago* species on dicotyledonous host plants, and *Haradaea* for species of *Microbotryaceae* parasitizing seeds of host plants in the Caryophyllaceae. This last decision was also based on the results of Almaraz *et al.* (2002), who studied the ITS sequences of some smut fungi of dicotyledonous host plants. In their cladogram *Ustilago duriaeana* represented a separate group which would have been the basis for considering it a separate genus. However, the culture analyzed by Almaraz *et al.* was a *Cryptococcus* sp. (Tremellales) (M. Lutz and M. Kemler, pers. comm.). More recent molecular phylogenetic studies, based on a greater number of species, could not confirm the division of *Microbotryum* s. lat. into these genera, although there are groups, more or less well-supported within *Microbotryum*, but in other arrangements (comp. Kemler *et al.* 2006, Kemler *et al.* 2008). Until results of molecular studies, based on many species of *Microbotryum* support a division of this genus into natural groups, it is best to treat it in a larger sense.

Microbotryum includes 94 species infecting hosts in ten families: Asteraceae, Caryophyllaceae, Dipsacaceae, Gentianaceae, Lamiaceae, Lentibulariaceae, Onagraceae, Polygonaceae, Portulacaceae and Primulaceae. Among the c. 28 species that infect hosts in the Caryophyllaceae, about 20 infect the anthers or flowers, 8 the seeds.

Key to the taxa of the order Microbotryales

. Microbotryaceae (2)	1. Mature septa poreless; spores with violet tint. On dicots
stilentylomataceae (5)	— Septa with simple pore; spores yellow or yellowish red. On monocots
Zundeliomyces	2. Spores of two types
	— Spores of the same type
	3. Peridium and columella in the sori present; spores at first catenate, joined by disjunctors
4	— Peridium and columella absent; spores not catenate
	4. Spores produced in lunate cavities and mixed with filaments
	— Spores not so
	5. Sori in hypertrophied spikelets of Cyperaceae, filled with orange-yellow spore balls
6	— Sori not hypertrophied
yaline to pale	6. Sori as leaf-spots on Poaceae; spores embedded in the host tissue, not powdery, single, h
Ustilentyloma	yellow
7	— Sori not as leaf-spots; spores powdery, pale golden-yellow to rusty brown
	7. Sori in the seeds of Cyperaceae and Juncaceae; spores single
	— Sori in the stems of Poaceae; spores in balls

HOST PLANTS OF THE SMUT FUNGI

The smut fungi are, with a few exceptions, plant parasitic fungi, mainly on angiosperms, especially on monocots. It is remarkable that no smut fungus is known on the large family of Orchidaceae, with about 20,000 species, or on members of the Zingiberales and Arecales. A saprobic smut, *Tilletiaria*, is known only from culture. Three smut fungi are known that parasitize Pteridophyta: a species of *Exoteliospora* on Osmundaceae (*Osmunda*) and two species of *Melaniella* on Selaginellaceae (*Selaginella* spp.). Two species of *Uleiella* are known occurring on gymnosperms, Araucariaceae (*Araucaria* spp.). The zoophilic *Malassezia* (Malasseziales, Exobasidiomycetidae), of which the sexual phase is unknown, produces the superficial skin lesions of humans, known as Pityriasis versicolor.

Of the c. 1700 species of "classical" smut fungi c. 885 species (= 52%) are on Poaceae, followed by 250 species on Cyperaceae (14%), 113 on Asteraceae (6.6%), 53 on Polygonaceae (3.1%), 53 on Ranunculaceae (3.1%), 42 on Liliaceae s. lat. (2.5%), 32 on Caryophyllaceae (1.8%), 24 on Fabaceae (1.4%), 23 on Restionaceae (1.4%), 21 on both Juncaceae and Scrophulariaceae (1.2%). Only one species each is known on Bromeliaceae, Centrolepidaceae, Droseraceae and Ruppiaceae. It is interesting that the teliospore-forming Ustilaginomycetes, with few exceptions, are parasites of herbaceous, non-woody plants, while those lacking teliospores (Microstromatales, Exobasidiales) mostly parasitize woody plants. Smut fungi occurring on woody plants are: Geminago (1 sp.) on Triplochiton (Sterculiaceae), Mundkurella (5 spp.) on four genera in the Araliaceae, Pericladium (3 spp.) on Grewia (Malvaceae) and Uleiella (2 spp.) on Araucaria (Araucariaceae).

Some genera of smut fungi are restricted to a certain host plant genus or family. A few genera are polyphagous on members of several host plant families, including mono- and dicotyledonous ones.

Monocotyledonous plants. Twenty four smut genera occur only on host plants in the Poaceae. These are: Anomalomyces (2 sp.), Anthracocystis (126), Bambusiomyces (1), Conidiosporomyces (3 spp.), Eballistra (3), Franzpetrakia (3), Fulvisporium (1), Ingoldiomyces (1), Langdonia (8), Macalpinomyces (41), Moesziomyces (1), Neovossia (1), Oberwinkleria (1), Phragmotaenium (1), Salmacisia (1), Sporisorium (205), Stollia (5), Tilletia (180), Tolyposporella (c. 5), Tranzscheliella (17), Triodiomyces (5), Tubisorus (1), Ustilago (200) and Ustilentyloma (4). Twenty smut genera occur only on Cyperaceae: Anthracoidea (c. 100 spp.), Aurantiosporium (4), Cintractia s. str. (11), Cintractiella (2), Dermatosorus (6), Farysia (20), Farysporium (1), Kuntzeomyces (2), Leucocintractia (4), Moreaua (36), Orphanomyces (3), Parvulago (1), Pilocintractia (2), Planetella (1), Portalia (1), Schizonella (5), Shivasia (1), Testicularia (3), Trichocintractia (1) and Ustanciosporium (20). Two genera only on Juncaceae: Stegocintractia (6) and Tolyposporium (3). On Poaceae and Cyperaceae occur the members of Jamesdicksonia (19 + 3 spp.). Cyperaceae and Juncaceae both are hosts of species of Bauerago (9), Entorrhiza (14) and Heterotolyposporium (2). Four smut genera are known on Liliaceae s. lat.: Antherospora (9), Clintamra (1), Gjaerumia (3) and Vankya (3); four genera on Eriocaulaceae: Eriocaulago (2), Eriocortex (1), Eriomoeszia (1) and Eriosporium (2); two genera on both Araceae: Entylomaster (2), Melanustilospora (2), and Restionaceae: Restiosporium (21) and Websdanea (1). One genus is known on Centrolepidaceae: Centrolepidosporium (1) and on Ruppiaceae: Flamingomyces (1).

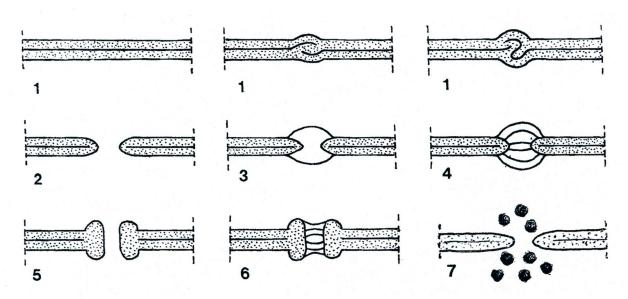
<u>Dicotyledonous</u> plants. Several small, often unispecific smut genera are known on host plants belonging to a single dicotyledonous family. On **Aizoaceae**: Aizoago (2 spp.), Talbotiomyces (1); on **Araliaceae**: Mundkurella (5 spp.); on **Convolvulaceae**: Georgefischeria (4); on **Euphorbiaceae**: Ahmadiago (1); on **Fabaceae**: Erratomyces (5); on **Nymphaeaceae**: Rhamphospora (1); on **Oxalidaceae**: Melanoxa (2); on **Polygonaceae**: Liroa (1), Melanopsichium (2), Sphacelotheca (5), Zundeliomyces (1); on **Rosaceae**: Ustacystis (1); on **Sterculiaceae**: Geminago (1); on **Vitaceae**: Mycosyrinx (4). Talbotiomyces calosporus, the single species of this genus, occurs on members of **Aizoaceae**, **Molluginaceae** and **Portulacaceae**. Polyphagous smut genera on dicots are: Entyloma (with 172 species on 25 host plant families), Melanotaenium s. str. (9 species on 7 families), Microbotryum (94 species on 10 families), and Thecaphora (60 species on 16 families).

Mono- and dicotyledonous plants. Species of some smut genera are adapted to host plants in widely different families, both mono- and dicotyledonous ones. *Urocystis*, with 170 species on members of 31 host plant families, of which 16 are monocots and 15 dicots. Of four species of *Yelsemia* one is on a monocot and 3 are on dicots. About 50 smut fungi, belonging to genera in the Doassansiopsidaceae and Doassansiaceae, occur on most different, unrelated, monocotyledonous and dicotyledonous families but only aquatic or paludal plants, to which environment they are specifically adapted.

SEPTAL PORE AND HOST-PARASITE INTERACTION IN SMUT FUNGI

Modern, high-power electron microscopes and special laboratory techniques, elaborated during the second half of the last century, were the prerequisites for the study of the ultrastructure of fungi. Morphology of cell and spore walls, spindle pole bodies and especially of septal pores, and host-parasite interactions supply precious information usable for a more natural classification of the smut fungi (comp. Bauer, Oberwinkler & Vánky 1997). Whereas fruiting bodies of fungi may change to adapt to environmental conditions, often resulting in convergent evolution, septal pore morphology and host-parasite interaction are relatively stable, invariable characteristics that can help establish the relationship of larger groups and higher taxa. The septal pore and host-parasite interaction types occurring within the smut fungi (comp. also Bauer, Begerow, Oberwinkler, Piepenbring & Berbee, 2000), are schematically illustrated below.

Septal pore types of smut fungi



- 1. Mature septum without pore (Ustilaginales, Georgefischeriales, Microbotryaceae).
- 2. Simple pore without membrane cap (Ustilentylomataceae).
- 3. Simple pore with two membrane caps, no inner plates (Melanotaeniaceae, [Microstromatales], Entylomatales, Doassansiales, [Exobasidiales]).
- 4. Simple pore with two outer membrane caps and two inner, non-membranous plates closing the pore (Doassansiopsidaceae, Urocystidaceae).
- 5. Dolipore without pore cap or membranous plates (Entorrhizaceae).
- 6. Dolipore without pore cap, with membranous plates (Tilletiales).
- 7. Simple pore with Woronin bodies (Ascomycetes: Schroeteria, Restilago)

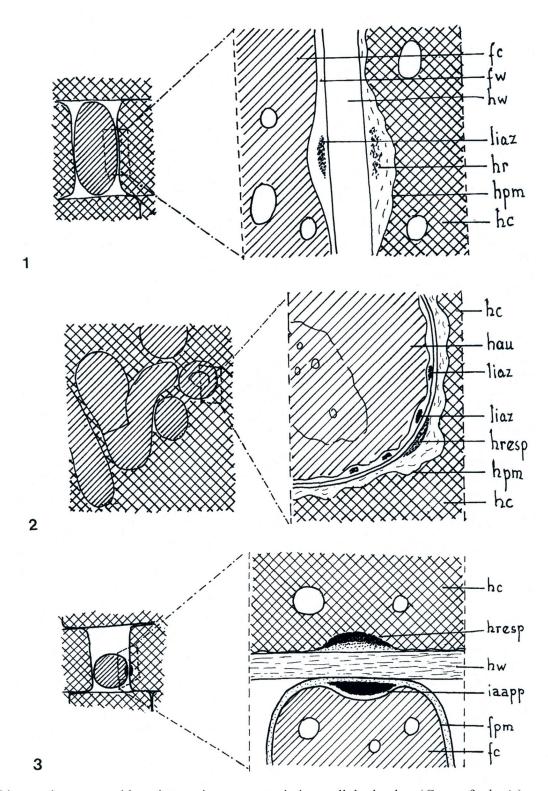
Cellular host-parasite interaction types of smut fungi

(Based on Bauer et al. 1997 & 2000)

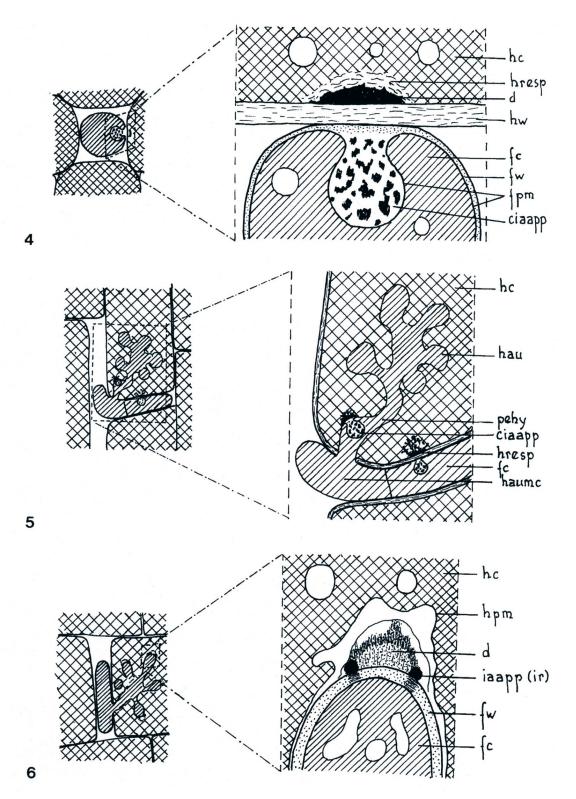
I. Local interaction zones.

- 1. **Local interaction zones** without interaction apparatus. They may be present in intercellular hyphae or in haustoria (Entorrhizomycetes, Georgefischeriales, Tilletiales [and Microstromatales]).
- a. Local interaction zones without interaction apparatus in intercellular hyphae (Tilletiales, Georgefischeriales) [Fig. 1].
 - b. Local interaction zones without interaction apparatus in haustoria (Entorrhizomycetes) [Fig. 2].
 - 2. Local interaction zones with interaction apparatus.
- A. Local interaction zones with <u>simple</u> interaction apparatus. Present only in intercellular hyphae (Entylomatales) [Fig. 3].
 - B. Local interaction zones with complex interaction apparatus.
- a. Local interaction zones with complex interaction apparatus containing **cytoplasmic compartments** (Doassansiales). It may be located
 - a/1. in intercellular hyphae (Doassansiaceae, Melaniellaceae) [Fig. 4], or
 - a/2. in intracellular hyphae and haustoria (Rhamphosporaceae) [Fig. 5].
- b. Local interaction zones with complex interaction apparatus producing **interaction rings**. May be located in intercellular hyphae or in haustoria [Exobasidiales, including Graphiolaceae] [Fig. 6].
- II. <u>Enlarged interaction zones</u>. May be present in intracellular hyphae, intercellular hyphae or in haustoria (Ustilaginomycetes).
- a. Enlarged interaction zones **in intracellular hyphae** (Ustilaginaceae and related families: Anthracoideaceae, Clintamraceae, Geminaginaceae, Glomosporiaceae, Uleiellaceae, Websdaneaceae) [Fig. 7].
 - b. Enlarged interaction zones in intercellular hyphae (Mycosyringaceae) [Fig. 8].
 - c. Enlarged interaction zones in haustoria (Urocystidales) [Fig. 9].

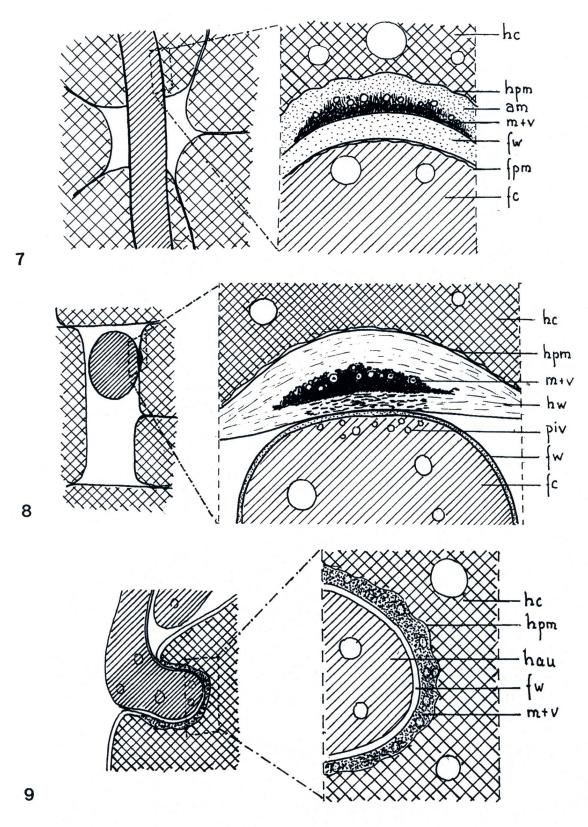
Abbreviations: am = appositional material; ciaapp = complex interaction apparatus; d = deposit; fc = fungal cell; fpm = fungal plasma membrane; fw = fungal wall; hau = haustorium; haumc = haustorial mother cell; hc = host cell; hpm = host plasma membrane; hresp = host response; hw = host wall; hau = haustorial mother cell; hc = host cell; hpm = host plasma membrane; hresp = host response; hw = host wall; hau = haustorial mother cell; hc = host cell; hpm = host plasma membrane; hresp = host response; hw = host wall; hau = haustorial mother cell; hc = host cell; hpm = host plasma membrane; hresp = host response; hw = host wall; hau = haustorial mother cell; hc = host c



- 1. Local interaction zones without interaction apparatus in intercellular hyphae (Georgefischeria).
- 2. Local interaction zones without interaction apparatus in haustoria (*Entorrhiza*).
- 3. Local interaction zones with simple interaction apparatus in intercellular hyphae (Entyloma).



- 4. Local interaction zones with complex interaction apparatus containing cytoplasmic compartments in intercellular hyphae (*Doassinga*).
- 5. Local interaction zones with complex interaction apparatus containing cytoplasmic compartments in intracellular hyphae and haustoria (*Rhamphospora*).
- 6. Local interaction zones with complex interaction apparatus producing interaction rings in haustoria [Exobasidium].



- 7. Enlarged interaction zones in intracellular hyphae (Anthracoidea).
- 8. Enlarged interaction zones in intercellular hyphae (*Mycosyrinx*).
- 9. Enlarged interaction zones in haustoria (Urocystis).

CLASSIFICATION OF SMUT FUNGI AND ALLIED TAXA

The nearly 1700 known species of "classical" basidiomycetous smut fungi, i.e. those possessing teliospores, are classified into one phylum, 2 subphyla, 4 classes, 8 orders, 27 families and 102 genera. Taxa within brackets are not considered smut fungi. Listed below are the main ultrastructural characters of the higher taxa of smut fungi; the known number of species within each genus (in parentheses); and the host plant families. Genera in bold face are treated in this book. [Comp. also Bauer, Oberwinkler & Vánky 1997, Begerow, Bauer & Oberwinkler 1998('1997'), Vánky 1999b, Piepenbring, Begerow & Oberwinkler 1999, Bauer, Begerow, Oberwinkler, Piepenbring & Berbee 2000, Bauer, Begerow, Nagler & Oberwinkler 2001, Vánky 2001b, Weiss, Bauer & Begerow, in Agerer *et al.* 2004]. Monocotyledonous hosts are indicated by Mo, and dicotyledonous hosts by Di.

CLASSIFICATION OF THE SMUT FUNGI

Kingdom FUNGI T.L. Jahn & F.F. Jahn ex R.T. Moore

[Phylum CHYTRIDIOMYCOTA, and some oher Phyla]

Phylum ASCOMYCOTA Caval.-Sm.

Taxa incertae sedis in Ascomycota:

Schroeteria G. Winter (6) Di (Scrophulariaceae).

Restilago Vánky (1) Mo (Restionaceae).

Phylum BASIDIOMYCOTA R.T. Moore

Subphyl. USTILAGINOMYCOTINA R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Host-parasite interactions with deposits of specific fungal vesicles.

Cl. Entorrhizomycetes Begerow, M. Stoll & R. Bauer

Local interaction zones and septal pores without membranous plates or caps. Haustoria present.

Ord. Entorrhizales R. Bauer & Oberw.

Dolipores and intracellular hyphae and spores.

Fam. Entorrhizaceae R. Bauer & Oberw.

Having characters of the Order Entorrhizales.

Entorrhiza C.A. Weber (14) Mo (Cyperaceae, Juncaceae).

Taxon incertum sedis in Entorrhizomycetes:

Talbotiomyces Vánky, R. Bauer, Begerow (1) Di (Molluginaceae, Aizoaceae, Portulacaceae).

Cl. Exobasidiomycetes Begerow, M. Stoll & R. Bauer

Local interaction zones. Septa have pores with membranous plates or caps or they are poreless at maturity.

[Ord. Ceraceosorales Begerow, M. Stoll & R. Bauer]

[Ceraceosorus B.K. Bakhsi]

Ord. Georgefischeriales R. Bauer, Begerow & Oberw.

Mature septa poreless.

Fam. Georgefischeriaceae R. Bauer, Begerow & Oberw.

Holobasidia and ballistospores.

Georgefischeria Thirum. & Narash., emend. Gandhe (4) Di (Convolvulaceae).

Jamesdicksonia Thirum., Pavgi & Payak, emend. Raghunath, emend. J. Walker & R.G. Shivas, emend. R. Bauer, Begerow, A. Nagler & Oberw. (22) Mo (Cyperaceae, Poaceae).

Fam. Tilletiariaceae R.T. Moore

Phragmobasidia, ballisto-basidiospores.

Phragmotaenium R. Bauer, Begerow, A. Nagler & Oberw. (1) Mo (Poaceae).

Tilletiaria Bandoni & B.N. Johri (1) saprobic and numerous anamorph species.

Tolyposporella G.F. Atk. (5) Mo (Poaceae).

Fam. Eballistraceae R. Bauer, Begerow, A. Nagler & Oberw.

Holobasidia, gastroid basidiospores, and yeast.

Eballistra R. Bauer, Begerow, A. Nagler & Oberw. (3) Mo (Poaceae).

Fam. **Gjaerumiaceae** R. Bauer, M. Lutz & Oberw.

Dolipores.

Gjaerumia R. Bauer, M. Lutz & Oberw. (3) Mo (Liliaceae s. lat.).

[Ord. Malasseziales R.T. Moore, emend. Begerow, R. Bauer & Boeckhout]

[Zoophilic, with lipophilic yeast phase, with multilamellate cell wall, monopolar budding and helicoidal evagination of the plasma membrane. Sexual phase unknown]

[Malassezia Baillon]

[Ord. Microstromatales R. Bauer & Oberw.]

[Simple septal pores with membranous caps. Interaction apparatus and teliospores are lacking]

[Fam. Microstromataceae Jülich]

[Has the characters of the order]

[Microstroma Niessl, Rhodotorula spp. (mitosporic), Sympodiomycopsis (mitosporic)]

[Fam. Quambalariaceae Z.W. de Beer, Begerow & R. Bauer]

[Quambalaria J.A. Simpson (perhaps mitosporic)]

[Fam. Volvocisporiaceae Begerow, R. Bauer & Oberw.]

[Volvocisporium Begerow, R. Bauer & Oberw.]

Ord. Tilletiales Kreisel ex R. Bauer & Oberw.

Dolipores without caps, traversed by two membranous plates. Interaction apparatus lacking. Hyphae intercellular.

Fam. Tilletiaceae Tul. & C. Tul., emend. R. Bauer & Oberw.

In various organs, usually in ovaries of Poaceae.

Conidiosporomyces Vánky (3) Mo (Poaceae).

Ingoldiomyces Vánky (1) Mo (Poaceae).

Neovossia Körn., s. str. (1) Mo (Poaceae).

Oberwinkleria Vánky & R. Bauer (1) Mo (Poaceae).

Salmacisia D.R. Huff & A. Chandra (1) Mo (Poaceae).

Tilletia Tul. & C. Tul. (c. 180) Mo (Poaceae).

Fam. Erratomycetaceae Denchev

In vegetative organs of Fabaceae.

Erratomyces M. Piepenbr. & R. Bauer (5) Di (Fabaceae).

Ord. Entylomatales R. Bauer & Oberw.

Simple septal pores with membrane caps, teliospores, and interaction apparatus with homogenous contents. No haustoria.

Fam. Entylomataceae R. Bauer & Oberw.

Has the characters of the order.

Entyloma de Bary, s. str. (c. 180) Di (25 fam.).

[Tilletiopsis spp. (mitosporic)]

Ord. Doassansiales R. Bauer & Oberw.

Simple septal pores with membrane caps, teliospores, and complex interaction apparatus with inhomogeneous contents.

Fam. Melaniellaceae R. Bauer, Vánky, Begerow & Oberw.

Intercellular hyphae, simple septal pores with membrane caps. Haustoria absent. Spores pigmented. *Melaniella* R. Bauer, Vánky, Begerow & Oberw. (2) Lycophyta (Selaginellaceae).

Fam. **Doassansiaceae** (Azbukina & Karatygin) R.T. Moore ex P.M. Kirk, P.F. Cannon & J.C. David Intercellular hyphae. Haustoria absent. Spores unpigmented.

Burrillia Setch. (4) Mo (Alismataceae, Pontederiaceae).

Doassansia Cornu (12) Mo (5 fam.), Di (7 fam.).

Doassinga Vánky, R. Bauer & Begerow (1) Di (Callitrichaceae).

Entylomaster Vánky & R.G. Shivas (2) Mo (Araceae).

Heterodoassansia Vánky (8) Mo (Alismataceae), Di (Acanthaceae, Callitrichaceae, Lythraceae, Primulaceae, Ranunculaceae).

Nannfeldtiomyces Vánky (2) Mo (Sparganiaceae).

Narasimhania Thirum. & Pavgi, emend. Vánky (1) Mo (Alismataceae).

Pseudodermatosorus Vánky (2) Mo (Alismataceae).

Pseudodoassansia (Setch.) Vánky (2) Mo (Alismataceae, Limnocharitaceae).

Pseudotracya Vánky (1) Mo (Hydrocharitaceae).

Tracya H. & P. Sydow (2) Mo (Hydrocharitaceae, Lemnaceae).

Fam. Rhamphosporaceae R. Bauer & Oberw.

Intracellular hyphae and haustoria. Spores unpigmented.

Rhamphospora D.D. Cunn. (1) Di (Nymphaeaceae).

[Ord. Exobasidiales Henn.]

[Simple septal pores and complex interaction apparatus with ring. Teliospores lacking. Basidia produced singly or side by side]

[Fam. Brachybasidiaceae Gäum.]

[Brachybasidium Gäum., Dicellomyces L.S. Olive, Exobasidiellum Donk, Kordyana Racib., Meira (Mitosporic), Proliferobasidium J.L. Cunn.]

[Fam. Cryptobasidiaceae Malençon ex Donk]

[Acaromyces (mytosporic), Botryoconis H. & P. Sydow, Clinoconidium Pat., Coniodictyum Har. & Pat., Drepanoconis J. Schröter & Henn., Laurobasidium Jülich, Phacellula H. Sydow]

[Fam. Exobasidiaceae Henn.]

[Arcticomyces Savile, Exobasidium Woronin, Muribasidiospora Kamat & Rajendren]

[Fam. Graphiolaceae E. Fisch.]

[Graphiola Poit., Stylina H. Sydow]

Cl. Ustilaginomycetes R. Bauer, Oberw. & Vánky, emend. Begerow, M. Stoll & R. Bauer

Enlarged interaction zones. Septa have pores with membranous caps or they are poreless.

Ord. Urocystidales R. Bauer & Oberw.

Simple septal pores. Haustoria present.

Fam. Doassansiopsidaceae Begerow, R. Bauer & Oberw.

Simple septal pores with two membrane caps and two non-membranous inner plates closing the pore. Spores colorless.

Doassansiopsis (Setch.) Dietel (14) Mo (Alismataceae, Limnocharitaceae, Potamogetonaceae), Di Menyanthaceae, Nymphaeaceae).

Fam. Floromycetaceae M. Lutz, R. Bauer & Vánky

Simple septal pores with rounded pore lips, enclosed by two membrane caps. Spores pigmented, single or in balls, sterile cells lacking. In flowers of monocots.

Antherospora R. Bauer, M. Lutz, Begerow, Pi tek & Vánky (8) Mo (Hyacinthaceae).

Floromyces Vánky, M. Lutz & R. Bauer (1) Mo (Agavaceae).

Fam. Glomosporiaceae Cif., emend. Begerow, R. Bauer & Oberw.

Intracellular hyphae. Spores usually forming balls. Spore germination results in holobasidia or in septate or aseptate hyphae.

Thecaphora Fingerh., emend. Vánky (including Glomosporium, Kochmania, Sorosporium, Tothiella)

(61) Di (Amaranthaceae, Apiaceae, Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae,

Chenopodiaceae, Convolvulaceae, Fabaceae, Molluginaceae, Nyctaginaceae, Oxalidaceae,

Polygonaceae, Primulaceae, Rubiaceae, Solanaceae).

Fam. Mycosyringaceae R. Bauer & Oberw.

Intercellular hyphae. Basidium reduced to the teliospore.

Mycosyrinx Beck (4) Di (Vitaceae).

Fam. Urocystidaceae Begerow, R. Bauer & Oberw.

Simple septal pores with two membrane caps and two non-membranous inner plates closing the pore. Spores pigmented.

Flamingomyces R. Bauer, M. Lutz, Pi tek, Vánky & Oberw. (1) Mo (Ruppiaceae).

Melanoxa M. Lutz, Vánky & R. Bauer (2) Di (Oxalidaceae).

Melanustilospora Denchev (2) Mo (Araceae).

Mundkurella Thirum. (5) Di (Araliaceae).

Urocystis Rabenh. ex Fuckel (c. 170) Mo (Alliaceae, Amaryllidaceae, Alstroemeriaceae,

Asphodeliaceae, Colchicaceae, Convallariaceae, Cyperaceae, Eriospermaceae, Hyacinthaceae,

Hypoxidaceae, Iridaceae, Juncaceae, Liliaceae, Poaceae, Ruscaceae, Trilliaceae), Di (Apiaceae,

Brassicaceae, Dioscoreaceae, Ericaceae, Hydrophyllaceae, Orobanchaceae, Oxalidaceae,

Polemoniaceae, Primulaceae, Ranunculaceae, Rosaceae, Saxifragaceae, Scrophulariaceae, Solanaceae, Violaceae).

Ustacystis Zundel (1) Di (Rosaceae).

Vankya Ershad (3) Mo (Liliaceae s. str.).

Ord. Ustilaginales G. Winter, emend. R. Bauer & Oberw.

Poreless septa.

Fam. Anthracoideaceae Denchev.

Intracellular hyphae. Spores single or in balls, pigmented. On Cyperaceae & Juncaceae.

Anthracoidea Bref. (c. 100) Mo (Cyperaceae).

Cintractia Cornu, s. str. (11) Mo (Cyperaceae).

Dermatosorus K. Sawada ex L. Ling (6) Mo (Cyperaceae).

Farysia Racib. (20) Mo (Cyperaceae).

Heterotolyposporium Vánky (2) Mo (Cyperaceae, Juncaceae).

Moreaua T.N. Liou & H.C. Cheng (36) Mo (Cyperaceae).

Planetella Savile (1) Mo (Cyperaceae).

Schizonella J. Schröter (5) Mo (Cyperaceae).

Stegocintractia M. Piepenbr., Begerow & Oberw. (6) Mo (Juncaceae).

Tolyposporium Woronin ex J. Schröter (3) Mo (Cyperaceae, Juncaceae).

Trichocintractia M. Piepenbr. (1) Mo (Cyperaceae).

Tentatively also

Farysporium Vánky (1) Mo (Cyperaceae).

Kuntzeomyces Henn. ex Sacc. & P. Sydow (2) Mo (Cyperaceae).

Leucocintractia M. Piepenbr., Begerow & Oberw. (4) Mo (Cyperaceae).

Orphanomyces Savile (3) Mo (Cyperaceae).

Pilocintractia Vánky (2) Mo (Cyperaceae).

Portalia V. González, Vánky & G. Platas (1) Mo (Cyperaceae).

Shivasia Vánky, M. Lutz & Pi tek (1) Mo (Cyperaceae).

Testicularia Klotzsch (3) Mo (Cyperaceae).

Ustanciosporium Vánky, emend. M. Piepenbr. (20) Mo (Cyperaceae).

Fam. Cintractiellaceae Vánky

Haustoria present.

Cintractiella Boedijn (2) Mo (Cyperaceae, subfam. Mapanioideae).

Fam. Clintamraceae Vánky

Intracellular hyphae, and the characters of *Clintamra*.

Clintamra Cordas & Durán (1) Mo (Liliaceae).

Fam. Geminaginaceae Vánky

Intracellular hyphae, and the characters of Geminago.

Geminago Vánky & R. Bauer (1) Di (Sterculiaceae).

Fam. Melanotaeniaceae Begerow, R. Bauer & Oberw.

Simple pores with membrane caps, no inner plates.

Exoteliospora R. Bauer, Oberw. & Vánky (1) Pteridophyta (Osmundaceae).

Melanotaenium de Bary s. str. (9) Di (Adoxaceae, Campanulaceae, Euphorbiaceae, Haloragaceae, Lamiaceae, Rubiaceae, Scrophulariaceae).

Yelsemia J. Walker (4) Mo (Liliaceae), Di (Byblidaceae, Campanulaceae, Droseraceae).

Fam. Pericladiaceae Vánky

Intracellular hyphae, and characters of *Pericladium*.

Pericladium Pass. (3) Di (Malvaceae).

Fam. Uleiellaceae Vánky

Intracellular hyphae, and the characters of *Uleiella*.

Uleiella J. Schröter (2) Gymnospermae (Araucariaceae).

Fam. Ustilaginaceae Tul. & C. Tul. (1847), emend. R. Bauer & Oberw.

Intracellular hyphae.

Anthracocystis Bref. (126) Mo (Poaceae).

Langdonia McTaggart & R.G. Shivas (8) Mo (Poaceae).

Macalpinomyces Langdon & Full., emend. Vánky, s. lat. (41) Mo (Poaceae).

Melanopsichium Beck (2) Di (Polygonaceae).

Moesziomyces Vánky (1) Mo (Poaceae).

Parvulago R. Bauer, M. Lutz, Pi tek, Vánky & Oberw. (1) Mo (Cyperaceae).

[Pseudozyma (mitosporic)]

Sporisorium Ehrenb. ex Link, emend. McTaggart & R.G. Shivas (205) Mo (Poaceae).

Stollia McTaggart & R.G. Shivas (5) Mo (Poaceae).

Triodiomyces McTaggart & R.G. Shivas (5) Mo (Poaceae).

Tubisorus Vánky & M. Lutz (1) Mo (Poaceae).

Ustilago (Pers.) Roussel (c. 200) Mo (Poaceae).

Tentatively also

Bambusiomyces Vánky (1) Mo (Poaceae).

Franzpetrakia Thirum. & Pavgi (3) Mo (Poaceae).

Tranzscheliella Lavrov (17) Mo (Poaceae).

Fam. Websdaneaceae Vánky

Intracellular hyphae, and the characters of Websdanea.

Restiosporium Vánky (21) Mo (Restionaceae).

Websdanea Vánky (1) Mo (Restionaceae).

Taxa incertae sedis in the Ustilaginales:

Ahmadiago Vánky (1) Di (Euphorbiaceae).

Aizoago Vánky (2) Di (Aizoaceae).

Anomalomyces Vánky, M. Lutz, R.G. Shivas, emend. Vánky & R.G. Shivas (2) Mo (Poaceae).

Centrolepidosporium R.G. Shivas & Vánky (1) Mo (Centrolepidaceae).

Eriocaulago Vánky (2) Mo (Eriocaulaceae).

Eriocortex Vánky & R.G. Shivas (1) Mo (Eriocaulaceae).

Eriomoeszia Vánky (1) Mo (Eriocaulaceae).

Eriosporium Vánky (2) Mo (Eriocaulaceae).

Subphyl. **PUCCINIOMYCOTINA** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Cl. Microbotryomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Host-parasite interactions without deposits of specific fungal vesicles.

Ord. Microbotryales R. Bauer & Oberw.

Fam. Microbotryaceae R.T. Moore

Poreless septa. Teliospores mostly violet-tinted. On dicots.

Liroa Cif. (1) Di (Polygonaceae).

Microbotryum Lév., emend. G. Deml & Oberw., emend. G. Deml & Prillinger, emend. Vánky (94) Di (Asteraceae, Caryophyllaceae, Dipsacaceae, Gentianaceae, Lamiaceae, Lentibulariaceae, Onagraceae,

Polygonaceae, Portulacaceae, Primulaceae).

Sphacelotheca de Bary (5) Di (Polygonaceae). *Zundeliomyces* Vánky (1) Di (Polygonaceae).

Fam. Ustilentylomataceae R. Bauer & Oberw.

Septa with simple pores lacking caps. Teliospores yellow. On monocots.

Aurantiosporium M. Piepenbr., Vánky & Oberw. (4) Mo (Cyperaceae).

Bauerago Vánky (9) Mo (Commelinaceae, Cyperaceae, Juncaceae).

Fulvisporium Vánky (1) Mo (Poaceae).

Ustilentyloma Savile (4) Mo (Poaceae).

[Cl. **Pucciniomycetes** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.] [Subphyl. **AGARICOMYCOTINA** Dowell] [Cl. **Tremellomycetes** Dowell] [Cl. **Agaricomycetes** Dowell]

SYNONYMS, EXCLUDED GENERA, ANAMORPHS, ASCOMYCETOUS SMUTS

Of the c. 165 described genera, 40 are considered to be **synonyms**. These are: Angiosorus (= Thecaphora), Bauhinus (= Microbotryum), Cintractiomyxa (= Anthracoidea), Cornuella Setch. (= Tracya), Crozalsiella (=?Ustilago), Didymochlamys (= Kuntzeomyces), Elateromyces (= Farysia). (= Macalpinomyces), Endothlaspis (= ?Sporisorium), Ginanniella (= Urocystis), Glomosporium (= Thecaphora), Granularia (= Ustanciosporium), Haradaeā (= Microbotryum),Urocystis), Gymnocintractia (= Juliohirschhornia (= ?Ustilago/Sporisorium), Kochmania (= Thecaphora), Lundquistia (= Anthracocystis), Milleria Peck (= Testicularia), Mycosarcoma (= Ustilago), Necrosis (= Ustilago), Perichlamys (= Kuntzeomyces), Pericoelium (= Ustilago), Poikilosporium (= Thecaphora), Polycystis (= Urocystis), Polysaccopsis (= Urocystis), Schinzia Nägeli (= Entorrhiza), Setchellia (= Doassansia), Sorosporium (= Thecaphora), Stereosorus (= Burrillia), Tolypoderma (= Moesziomyces), Tolyposporidium (= Moesziomyces), Tothiella (= Thecaphora), Tuburcinia (= Urocystis), Ulea (= Uleiella), Ustilagidium (= Ustilago), Vossia Thümen (= Neovossia), Whetzelia Zundel (= Ustacystis), Xylosorium (= Pericladium), Yenia (= Ustilago), Zundelula (= Dermatosorus). Others have been excluded from the smuts (Bryophytomyces, Kweilingia, Sorodiscus, Sporophaga, Ustilaginoidea, Ustilagopsis). There are also ten anamorph genera: Ascomyces (= p.p. Ginanniella = Urocystis), Crotalia Liro (= Anthracoidea), Doassansiella Zambett. (= Doassansiopsis), Entylomella Höhnel (= Entyloma), Paepalopsis (Paipalopsis) Kühn (= Urocystis), Rhombiella Liro (= Tothiella = Thecaphora), Savulescuella Cif. (= Doassansia, Tracya), Thecaphorella H. & I. Scholz (= Thecaphora), Tilletiella Zambett. (= Tilletia), Tracvella Zambett. (= Tracva). Ascmoycetous smut genera are Restilago and Schroeteria.

KEY TO THE GENERA OF SMUT FUNGI BASED ON HOST PLANT FAMILIES

KEY TO THE GENERA OF SMUT FUNGI BASED ON HOST PLANT FA	WILLES
On Acanthaceae . Spore balls embedded in the host tissue of aquatic plants.	
1. Spore balls composed of spores surrounded by a cortex of sterile cells of the same type	Doassansia
- Spore balls composed of spores surrounded by a cortex of two types of sterile cells	Heterodoassansia
On Adoxaceae. Spores solitary, dark pigmented, embedded in the host tissue	
On Agavaceae (Liliaceae s. lat.). Sori in the flowers; spores forming permanent spore balls	Floromyces
On Aizoaceae	
1. Sori forming galls on the roots; spores intracellular	Talbotiomyces
- Sori forming pustules on vegetative parts and fruits; spores not intracellular	Aizoago
On Alismataceae. Spore balls embedded in the host tissue of aquatic plants	
1. Spore balls without cortex, consisting of parenchymatous fungal tissue of sterile cells in which	
the spores are scattered	Burrillia
- Spore balls with cortex of sterile cells	
2. Spore balls lobed and also containing cavities	
Spore balls not lobed, compact, without cavities	
3. Central part of the spore balls composed of hyphae; spores situated between these and the cortex	
- Central part of the spore balls not composed of hyphae	
4. Central part of the spore balls composed of parenchymatous sterile cells only; spores situated	
between these and the cortex	Dogssansionsis
Central part of the spore balls composed of spores or also of sterile cells	
5. Central part of the spore balls composed of spores only	
 Central part of the spore balls composed of spores scattered in a network of sterile fungal cells 	
6. Cortical cells of one kind, not ornamented	
- Cortical cells of two types: external, small, not ornamented, and internal, larger, ornamented	Doussansia
on their inner surface	Ustanadanasansia
On Alliaceae. Spores in balls surrounded by sterile cells	
On Amaranthaceae. Spores in balls, sterile cells absent	
On Amaryllidaceae. Spores in balls surrounded by sterile cells	
On Anthericaceae. Spores single, pigmented, with two light-colored polar caps	Yelsemia
On Apiaceae.	
1. Spores single, embedded in the host tissue	
- Spores in balls; spore mass powdery	
2. Spore balls surrounded by sterile cells	
- Spore balls formed by spores only	Thecaphora
On Araceae.	
1. Spores dark, single, embedded in the host tissue	
 Spores pale, forming balls, embedded in the host tissue 	
On Araliaceae. Spores one to several-celled, mixed with sterile cells	
On Araucariaceae. Sori on the surface of inflorescence; one to several spores enclosed by a foveolate	coat
On Asphodelaceae (Liliaceae s. lat.).	
1. Spores in balls surrounded by sterile cells, powdery	Urocystis
 Spores single, embedded in the leaf tissue 	Gjaerumia
On Asteraceae.	
1. Spores in balls	Thecaphora
- Spores solitary	
2. Spores violet tinted, powdery	
- Spores not violet tinted, embedded in the host tissue	Entvloma
On Berberidaceae. Spores solitary, pale, embedded in the host tissue	
On Boraginaceae.	,
1. Spores solitary, hyaline, embedded in the host tissue	Entvloma
- Spores in balls, pigmented, powdery	
On Brassicaceae.	
Spores in balls surrounded by sterile cells	Urocvetie
- Spores in balls (but solitary in <i>T. capensis</i> and <i>T. thlaspeos</i>); no sterile cells	
On Butomaceae. Spore balls formed of spores surrounded by a cortex of sterile cells, embedded in the	
host tissue of aquatic plants	
•	
On Byblidaceae. Spores single, pigmented, with two light-colored polar caps	reisemia

On (Callitrichaceae.	
1.	Spores solitary, embedded in the host tissue of aquatic plants	Doassinga
_	Spores in balls surrounded by a cortex of two types of sterile cells, embedded in the host tissue	
	of aquatic plants	Heterodoassansia
On (Campanulaceae.	
1.	Spores in balls, pale colored, embedded in the host tissue of aquatic plants	
-	Spores single, pigmented, not on aquatic plants	
2.	Spores powdery, with two light-colored polar caps	
_	Spores embedded in the host tissue, not powdery, without polar caps	Melanotaenium
On (Caryophyllaceae.	161
1.	Spore mass violet; spores single	
-	Spore mass not violet; spores forming balls	
	Centrolepidaceae. Sori in the seeds of Centrolepis	Centrolepidosporium
	Chenopodiaceae.	
1.	Spores solitary, hyaline, embedded in the host tissue	
-	Spores in balls, pigmented, powdery	
	Colchicaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells	
	Commelinaceae. Sori in the seeds; spores solitary, powdery, golden brown	
	Convallariaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells	Urocystis
	Convolvulaceae.	m i
1.	Sori in the seeds; spores in balls, powdery	
_	Sori in the leaves or stems; spores embedded in the host tissue, not powdery	2
2.	Spores firmly agglutinated in indefinite masses; spore wall thick, multilayered	
-	Spores single; spore wall relatively thin; not multilayered	Entyloma
	Cyperaceae.	
1.	Two different types of spores present in the same sorus: small, hyaline, single spores mixed	TT 1
	with large, pigmented spore balls	
_	Spores of the same kind	
2.	Spores single	
_	Spores in pairs or in balls; sometimes in groups or single	
3.	Spores embedded in the host tissue	
_	Spores not embedded in the host tissue	
4.	Sori forming dark spots on leaves and stems	
_	Sori as galls on roots; spore mass pale	
5.	Spores mixed with fascicles of sterile fungal filaments; sori in the flowers	
_	Spores not mixed with fascicles of sterile fungal filaments	
6.	Spore wall separated into two layers by a hyaline, gelatinous mass	
_	Spore wall not separated into two layers.	
7.	Sori as orange yellow or reddish brown, powdery mass in the seeds; spores single	
- 0	Sori as black, agglutinated or semi-powdery masses in various organs of the host plants	
8.	Sori as black crusts on the leaves; spores single or in balls	
_	Sori not so	
9.		
10	Sori not so	
10.	Sori not so	
11	Sori around the seeds ("nutlets"); spores single; basidium 2-celled	
11.	Sori in various organs of the host plants; spores single, rarely in balls; basidium 4-celled	
12.	Spores with a dark equatorial band and two light-colored polar areas	
12.	Spores uniformly pigmented	
13.	Sori usually with sterile stroma surrounding internodes of the culms or floral pedicels,	ucoidea
13.	rarely the apex of sterile spikelets	14
	Sori not so	
14.	Infection systemic, host plants sterile	
- 14.	Infection localized, host plants not sterile	
15.	Sori in some spikelets of an inflorescence	
-	Sori in all spikelets or groups of spikelets of an inflorescence	17
_	bott in an spikelets of groups of spikelets of all inflorescence	1/

_	Sori with a sac-like peridium; spores powdery, mixed with long, hyphal cells	Trichocintractia
	Sori without sac-like peridium; spores agglutinated, mixed with gelatinized hyphae	
17.	On Scirpus; spores single	
_	On Rhynchospora, Bulbostylis, Cyperus, Scleria; spores single or in balls	Ustanciosporiun
18(2). Spores in pairs, the pairs rarely in balls, produced intraepidermally	
_	Spores in balls, not produced intraepidermally	
19.	Spore balls formed of spores and sterile cells	
_	Spore balls formed of spores only	
20.	The outer layer of the spore balls is formed by spores, surrounding the sterile cells	
_	The outer layer of the spore balls is formed by sterile cells, surrounding the spores	
21.	Spores and sterile cells reticulate; sori in the seeds	
_	Spores and sterile cells smooth or nearly so; in various organs of the host plants	
22(1	9). Spore mass black	
-	Spore mass yellowish, orange- or reddish brown	
23.	Sori around the floral axes traversed by fascicles of sterile hyphae; on Gahnia	Farysporium
_	Sori not so; not on Gahnia	
24.	Sori on the stems and in the flowers, not covered by peridium or floral envelopes	Tolyposporiun
_	Sori in the flowers only	25
25.	Sori exposed, globose, hard, at first covered by a thick, whitish peridium	Shivasia
_	Sori hidden by floral envelopes, granular powdery, no peridium	Moreauc
On I	Dioscoreaceae. Spores in balls surrounded by sterile cells	Urocystia
	Dipsacaceae. Spore mass violet tinted; spores single, powdery	
	Pracaenaceae (Liliaceae s. lat.). Sori forming a cover on the leaves and aborted inflorescence;	•
	spores single or in balls, composed of spores only	Clintamro
On I	Proseraceae. Spores single, pigmented, with two light-colored polar caps	
On I	Cricaceae. Spores in balls surrounded by sterile cells	Urocvsti
	Criocaulaceae.	
1.	Sori in the leaves and stems forming lead colored, compact striae	Tolyposporella
	Sori in the seeds	
	SOLI III THE SEEDS	
_ 2.		
_ 2. _	Spores single	Eriocaulago
_	Spores single	Eriocaulago
3.	Spores single	Eriocaulago
3. -	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex	Eriocaulage Eriosporium
3.	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells	Eriocaulage Eriosporium Eriomoesziu
3. - 4.	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells	Eriocaulago Eriosporium Eriomoeszia Eriocortex
- 3. - 4. - On l	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells	Eriocaulago Eriosporium Eriomoeszia Eriocortex
- 3. - 4. - On J	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae.	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocysti
- 3. - 4. - On J	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocysti
- 3. - 4. - On 1 On 1	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocysti
- 3 4 On 1 1 On 1	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Spores in the seeds, powdery Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores embedded in the host tissue, not powdery	Eriocaulage Eriosporium Eriomoeszia Eriocortes Urocystia Ahmadiage
- 3. - 4. - On 1 On 1	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores in balls, powdery	Eriocaulage Eriosporium Eriomoeszie Eriocortes Urocystie Ahmadiage Melanotaenium
- 3 4 On 1 1 On 1 1	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores in balls, powdery Spores single, embedded in the host tissue	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaeniun
- 3 4 On 1 1 On 1	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores in balls, powdery Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long.	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaeniun Thecaphoro
- 3 4 On I 1 On I 1 2	Spores single Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores in balls, powdery Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long. Sori as pale brown spots on leaves; spores less than 17 µm long.	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaeniun Thecaphoro Erratomyce
- 3 4 On 1 1 On 1 1 2 On 0	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Tabaceae. Spores in balls, powdery Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long Sori as pale brown spots on leaves; spores less than 17 µm long Gentianaceae. Spore mass violet tinted; spores single, powdery	Eriocaulage Eriosporium Eriomoesziu Eriocortes Urocystii Ahmadiage Melanotaenium Thecaphore Erratomyces Microbotryun
- 3 4 On 1 1 On 1 1 On 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	Spores single	Eriocaulago Eriosporium Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaenium Erratomyceo Entylomo Entylomo Entylomo
- 3 4 On I 1 On I 1 2 On	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores in balls, powdery Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long Sori as pale brown spots on leaves; spores less than 17 µm long Gentianaceae. Spores solitary, hyaline, embedded in the host tissue Gunneraceae. Spores solitary, dark pigmented, embedded in the host tissue	Eriocaulago Eriosporiun Eriomoeszio Eriocorte: Urocysti Ahmadiago Melanotaeniun Erratomyceo Entylomo Entylomo
- 3 4 On I 1 On I 1 On I I I I	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores embedded in the host tissue Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long. Sori as pale brown spots on leaves; spores less than 17 µm long Gentianaceae. Spore mass violet tinted; spores single, powdery Geraniaceae. Spores solitary, hyaline, embedded in the host tissue Gunneraceae. Spores solitary, dark pigmented, embedded in the host tissue Hyacinthaceae (Liliaceae s. lat.).	Eriocaulago Eriosporiun Eriomoeszio Eriocorte Urocysti Ahmadiago Melanotaeniun Erratomyce Entylomo Microbotryun Entylomo Melanotaeniun
- 3 4 On 1 On 1 1 On 1 On 0	Spores single	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaeniun Erratomyceo Entylomo Entylomo Melanotaeniun Microbotryun Entylomo Melanotaeniun
- 3 4 On 1 1 On 1 1 On 0 0 0 0 0 1 1 On 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Spores in the balls not mixed with sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Spores in the seeds, powdery Spores embedded in the host tissue, not powdery Spores in balls, powdery Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long Sori as pale brown spots on leaves; spores less than 17 µm long Gentianaceae. Spore mass violet tinted; spores single, powdery Geraniaceae. Spores solitary, hyaline, embedded in the host tissue Gunneraceae. Spores solitary, dark pigmented, embedded in the host tissue Hyacinthaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells, sori on leaves and stems. Spores single	Eriocaulago Eriosporiun Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaeniun Erratomyce Entylomo Entylomo Melanotaeniun Urocysti
- 3 4 On I 1 On I 1 On On On On On On On I I I I I I I I I	Spores single	Eriocaulago Eriosporium Eriomoeszio Eriocortex Urocystis Ahmadiago Melanotaenium Erratomyces Entylomo Microbotryum Entylomo Melanotaenium
- 3 4 On I 1 On On On On I 1 2 2 2 2 2 2 2	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery. Spores embedded in the host tissue, not powdery. Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long. Sori as pale brown spots on leaves; spores less than 17 µm long. Sentianaceae. Spore mass violet tinted; spores single, powdery. Geraniaceae. Spores solitary, hyaline, embedded in the host tissue Gunneraceae. Spores solitary, dark pigmented, embedded in the host tissue Hyacinthaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells, sori on leaves and stems. Spores powdery, in the flowers or on the leaves. Spores not powdery, embedded in the leaf tissue	Eriocaulago Eriosporium Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaenium Erratomyceo Entylomo Microbotryum Entylomo Melanotaenium Urocysti
- 3 4 On 1 1 On 1 1 On 0 0 0 0 0 0 1 1 2 On 0 2 2.	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery. Spores embedded in the host tissue, not powdery. Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long. Sori as pale brown spots on leaves; spores less than 17 µm long. Sentianaceae. Spore mass violet tinted; spores single, powdery. Geraniaceae. Spores solitary, hyaline, embedded in the host tissue Gunneraceae. Spores solitary, dark pigmented, embedded in the host tissue Hyacinthaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells, sori on leaves and stems. Spores powdery, in the flowers or on the leaves. Spores not powdery, embedded in the leaf tissue. Sori in the flowers	Eriocaulago Eriosporium Eriomoeszio Eriocortes Urocystio Ahmadiago Melanotaenium Ertatomyces Entylomo Microbotryum Entylomo Melanotaenium Urocystio
- 3 4 On I 1 On On On On I 1 2 3 3	Spores single Spores in balls Spore balls covered by a cortex Spore balls not covered by a cortex Spores in the balls mixed with and connected by sterile cells Spores in the balls not mixed with sterile cells Criospermaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells Cuphorbiaceae. Spores in the seeds, powdery Spores embedded in the host tissue, not powdery. Spores embedded in the host tissue, not powdery. Spores single, embedded in the host tissue Sori as dark spots on leaves; spores more than 17 µm long. Sori as pale brown spots on leaves; spores less than 17 µm long. Sentianaceae. Spore mass violet tinted; spores single, powdery. Geraniaceae. Spores solitary, hyaline, embedded in the host tissue Gunneraceae. Spores solitary, dark pigmented, embedded in the host tissue Hyacinthaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells, sori on leaves and stems. Spores powdery, in the flowers or on the leaves. Spores not powdery, embedded in the leaf tissue	Eriocaulago Eriosporium Eriosporium Eriomoeszia Eriocortex Urocystis Ahmadiago Melanotaenium Ertatomyces Entyloma Microbotryum Entyloma Melanotaenium Urocystis

On Hydrophyllaceae. Spores in balls surrounded by sterile cells. On Hypoxidaceae (Amaryllidaceae s. lat.). Spores in balls surrounded by sterile cells On Juncaceae. 1. Sori forming galls on the roots. Sori otherwise Sori otherwise Spores in balls Spores single Spores single Spores single Spores single Spore balls permanent, surrounded by sterile cells Urocystis Spore balls loose, composed of spores only Asmall, hyaline spores present between the spore balls Spore mass golden-brown; spores lemon- or orange-yellow Spore mass golden-brown; spores lemon- or orange-yellow Bauerago Spore mass dark pigmented, embedded in the host tissue Melanotaenium Spore mass violet tinted, powdery On Lemiaceae. Spore balls embedded in the host tissue of aquatic plants Tracya On Lentibulariaceae. Spore mass violet tinted; spores single, powdery Microbotryum On Liliaceae s. Str. Spores single, sterile cells between the spores present Urocystis Spores single, sterile cells between the spores present Urocystis Spores single, sterile cells between the spores single, powdery Microbotryum On Linnanthaceae. Spore solitary, hyaline, embedded in the host tissue Doassansiopsis Spore balls composed of a central mass of sterile cells surrounded by spores and an outer, cortical layer of sterile cells Doassansiopsis Spore balls composed of a central mass of branched hyphae in which the spores are scattered, surrounded by a cortex of sterile cells Pseudodoassansia On Linnaceae. Spores solitary, hyaline, embedded in the host tissue Entyloma On Linnaceae. Spores solitary, hyaline, embedded in the host tissue Entyloma
On Iridaceae. Spores in balls surrounded by sterile cells. Or Juncaceae. 1. Sori forming galls on the roots. Sori otherwise. Spores in balls. Spores single. Spores single. Spore balls permanent, surrounded by sterile cells. Spore balls permanent, surrounded by sterile cells. Spore balls loose, composed of spores only. Small, hyaline spores present between the spore balls. Heterotolyposporium Small, hyaline spores absent between the spore balls. Tolyposporium Spore mass golden-brown; spores lemon- or orange-yellow. Bauerago Spore mass black; spores reddish brown Stegocintractia On Lamiaceae. Spore mass dark pigmented, embedded in the host tissue. Melanotaenium Spore mass violet tinted, powdery. Microbotryum On Lemnaceae. Spore balls embedded in the host tissue of aquatic plants. Tracya On Lentibulariaceae. Spore mass violet tinted; spores single, powdery. Microbotryum On Liliaceae s. str. Spores in balls, surrounded by sterile cells. Lurocystis Spores single, sterile cells between the spore present. Luncystis Spores single, sterile cells between the spores present. Luncystis Spores single, sterile cells between the spores present. Luncystis Spore balls composed of a central mass of sterile cells surrounded by spores and an outer, cortical layer of sterile cells. Spore balls composed of a central mass of branched hyphae in which the spores are scattered, surrounded by a cortex of sterile cells. Pseudodoassansia
1. Sori forming galls on the roots
Sori otherwise
2. Spores in balls
Spore single
3. Spore balls permanent, surrounded by sterile cells
- Spore balls loose, composed of spores only
4. Small, hyaline spores present between the spore balls
Small, hyaline spores absent between the spore balls
5. Spore mass golden-brown; spores lemon- or orange-yellow
Spore mass black; spores reddish brown
On Lamiaceae. 1. Spore mass dark pigmented, embedded in the host tissue
1. Spore mass dark pigmented, embedded in the host tissue
- Spore mass violet tinted, powdery
On Lentibulariaceae. Spore balls embedded in the host tissue of aquatic plants. On Lentibulariaceae. Spore mass violet tinted; spores single, powdery. On Liliaceae s. str. 1. Spores in balls, surrounded by sterile cells. Spores single, sterile cells between the spores present. On Limnanthaceae. Spores solitary, hyaline, embedded in the host tissue. On Limnocharitaceae. Spore balls embedded in the host tissue of aquatic plants. 1. Spore balls composed of a central mass of sterile cells surrounded by spores and an outer, cortical layer of sterile cells. Doassansiopsis Spore balls composed of a central mass of branched hyphae in which the spores are scattered, surrounded by a cortex of sterile cells. Pseudodoassansia
On Liliaceae s. str. 1. Spores in balls, surrounded by sterile cells
On Liliaceae s. str. 1. Spores in balls, surrounded by sterile cells
1. Spores in balls, surrounded by sterile cells
 Spores single, sterile cells between the spores present
On Limnanthaceae. Spores solitary, hyaline, embedded in the host tissue
On Limnocharitaceae. Spore balls embedded in the host tissue of aquatic plants. 1. Spore balls composed of a central mass of sterile cells surrounded by spores and an outer, cortical layer of sterile cells
 Spore balls composed of a central mass of sterile cells surrounded by spores and an outer, cortical layer of sterile cells
layer of sterile cells
 Spore balls composed of a central mass of branched hyphae in which the spores are scattered, surrounded by a cortex of sterile cells
surrounded by a cortex of sterile cells
On Lobeliaceae. Spores solitary, hyaline, embedded in the host tissue
On Malvaceae. Spores solitary, hyaline, embedded in the host tissue
On Melanthiaceae (Liliaceae s. lat.). Sori as dark leaf spots; spores embedded in the host tissue
On Menispermaceae. Spores solitary, hyaline, embedded in the host tissue
On Menyanthaceae . Spores solitary, hyanne, embedded in the host tissue of aquatic plants.
1. Spore balls composed of a central mass of spores surrounded by a cortex of sterile cells
 Spore balls composed of a central mass of spores surrounded by the spores and an outer,
cortical layer of sterile cells
On Molluginaceae.
1. Sori on the roots forming galls; spores single
- Sori in the capsules, not forming galls; spores in balls
On Myrtaceae . Spores solitary, hyaline, embedded in the host tissue
On Nyctaginaceae. Spores in balls
On Nymphaeaceae. Spores and spore balls embedded in the host tissue of aquatic plants.
1. Spores in permanent balls, composed of a central mass of sterile cells surrounded by the spores
and an outer, cortical layer of sterile cells
- Spores single, lemon-shaped, with a papilla and an appendage
On Onagraceae.
1. Spores without violet tint, in permanent balls, embedded in the host tissue of aquatic plants
- Spores with a violet tint, single, powdery, not on aquatic plants
On Orobanchaceae. Spores in balls surrounded by sterile cells
On Osmundaceae. Sori external on hypertrophied, deformed leaves, cinnamon brown
On Oxalidaceae.
1. Spores in balls surrounded by sterile cells
- Spores single, sterile cells absent
2. Spores embedded in the host tissue, not powdery
- Spores powdery (as an exception not forming balls: T. capensis & T. oxalidis)
3. Spores pale Entyloma

_	Spores dark	Melanoxa
On	Papaveraceae. Spores solitary, hyaline, embedded in the host tissue	Entvloma
On	Plantaginaceae. Spores solitary, hyaline, embedded in the host tissue	Entyloma
On	Poaceae.	
For	a key of the genera Anthracocystis, Langdonia, Stollia and Triodiomyces see McTaggart et al.	2012c:131
1.	Spores mixed with groups of Y-shaped conidia	Conidiosporomyces
_	Spores not mixed with conidia	2
2.	Spores mixed with long, sterile fungal chains	Franzpetrakia
_	Spores not mixed with sterile fungal chains	3
3.	Spores in spore balls	4
_	Spores solitary or in groups, not in balls	10
4.	Spore balls composed of spores and sterile cells	5
_	Spore balls composed of spores only	6
5.	Spore balls surrounded by sterile cells	Urocystis
_	Sterile cells scattered between the spores in the balls	Moesziomyces
6.	Spore balls golden-yellow; no sterile cells between the balls	Fulvisporium
_	Spore balls brown	7
7.	Sterile cells between the balls lacking; spore wall very thick, multilayered	8
_	Sterile cells between the spore balls usually present; spore wall thinner, not multilayered	9
8.	Sori in the axis of the spikes, tubular; spores with an inner spore released in squashed spores	Tubisorus
_	Sori on the leaves and leaf sheaths; spores without an inner spore	Tolyposporella
9.	Spore balls covered by hard, dark cortex. Sterile cells between the spore balls variable in	
	morphology and frequency, one or more types	Anomalomyces
-	Spore balls not covered by cortex. Sterile cells between the spore balls one kind, numerous, few	v or lacking Sporisorium
10(.	3). Sori as leaf spots, rarely as crusts; spores embedded in the host tissue, not powdery	11
_	Spores powdery	14
11.	Sori yellow or pale brown; spores subhyaline	
-	Sori dark, blackish brown; spores dark pigmented	
12.	Basidia 4-celled, with ballistosporic basidiospores on lateral sterigmata	Phragmotaenium
12	Basidia 1-celled, with apical basidiospores	13
13.	Ballistospores present	
146	Ballistospores absent	Eballistra
14(10). Sori mostly in ovaries; spores large, usually >16 μm	
16	Sori in various parts of the host plants; spores small to medium-sized	18
15.	Spores elongate, foveolate, with a conspicuous hyaline appendage	Neovossia
16	Spores globoid, otherwise ornamented, appendage lacking or short, papilla-like	
16.	Spores with a dark, pigmented ring; basidia reduced to the spores	Oberwinkleria
_ 17.	Spores without a dark, pigmented ring; basidia not reduced to the spores	
1 /.	Spores peculiarly ridged; basidiospores 1-2, ballistosporic	Ingoldiomyces
	or spines, rarely smooth; basidiospores several, not ballistosporic	T:11-4: / C-1
180	4). Sori naked surrounding stems or floral axis; spores usually small, <8 μm	Tilletia / Saimacisia
-	Sori not so; spores usually larger	19
19.	Basidium short, aseptate, holobasidium with a few, large, apical basidiospores; on subfam. Ban	ahusaidaaa
1).	Busidiani short, aseptate, norobasidiani with a rew, targe, apiear basidiospores, on subtain. Ban	Rambusiomy as
_	Basidium septate, phragmobasidium with lateral and terminal, ovoid basidiospores; not on Ban	husoidese
	Sustain separe, pinaginosasianin with lateral and terminal, ovoid basidiospores, not on Ban	
20.	Spores single or in groups, mixed with sterile cells	
_	Spores single, not mixed with sterile cells	
On	Polemoniaceae.	Usungo
1.	Spores single, embedded in the host tissue, not powdery	Entyloma
_	Spores in balls surrounded by sterile cells, powdery	
On	Polygonaceae.	Orocysus
1.	Spores hyaline, of two types: thin-walled, ridged, and thick-walled, tuberculate	7undalionwace
_	Spores pigmented, of the same kind	Zunuenomyces
2.	Spores in balls	Thecanhora
_	Spores single	
	1 0-	

	Sori forming multilocular galls; spores embedded in a gelatinous mass	
	Peridium and columella present; spores when young in chains	
	Peridium and columella absent; spores when young not in chains	
	Filaments present in the sori; spores produced in cavities in the flowers or in galls on the stems	
	Filaments absent in the sori; spores not produced in cavities	
	ontederiaceae. Spore balls embedded in the host tissue of aquatic plants.	
1.	Spore balls composed of sterile cells in which the spores are scattered	Burrillia
-	Spore balls composed of spores surrounded by a cortex of sterile cells	Doassansia
On P	ortulacaceae.	
1.	Sori on the roots forming galls; spores intracellular, not powdery	Talbotiomyces
_	Sori not on the roots; spores not intracellular, powdery	Microbotryum
On P	otamogetonaceae. Spore balls embedded in the host tissue	Doassansiopsis
On P	rimulaceae.	
1.	Spores single	2
-	Spores in balls	3
2.	Spores embedded in the host tissue, not powdery, pale colored	Entyloma
_	Spores not embedded in the host tissue, powdery, pigmented, with a violet tint	Microbotryum
	Spore balls embedded in the host tissue; spores pale yellow	
_	Spore balls not embedded in the host tissue, powdery; spores pigmented	4
	Spore balls composed of spores surrounded by sterile cells	
	Spore balls composed of spores only	Thecaphora
	anunculaceae.	
	Spores single; embedded in the host tissue	
_	Spores in balls	3
	Spores pale	
	Spores dark	
	Spore balls embedded in the host tissue of aquatic plants; spores pale yellow	
-	Spore balls powdery; spores pigmented	Urocystis
	estionaceae s. lat.	
	Sori as bullate striae on the culms of sterile plants	
_	Sori in the seeds	Restiosporium
	osaceae.	
	Spores in balls, covered by sterile cells	•
	Spores single or in loose balls, sterile cells absent	Ustacystis
	ubiaceae.	
	Spores solitary, embedded in the host tissue	
	Spores in balls, powdery	
	uppiaceae. Sori in basal part of the leaves and in the rhizomes as dark, swollen striae	
	uscaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells	Urocystis
	axifragaceae.	
	Spores single, embedded in the host tissue, not powdery	
	Spores in balls surrounded by sterile cells, powdery	Urocystis
	crophulariaceae.	
	Spores in balls	
	Spores single, embedded in the host tissue	
	Spore balls embedded in the host tissue; spores pale	
	Spore balls not embedded in the host tissue, powdery; spores pigmented	
	Spores	
	Spores dark	
	elaginellaceae. Sori as black spots on leaves or stems; spores single, dark, embedded in the host tolanaceae.	assue Melaniella
	Spores pale, single, embedded in the host tissue	Entyloma
	Spores pigmented, in balls, powdery	
	Spore balls composed of spores surrounded by sterile cells	
	Spore balls composed of spores only	-

	On Sparganiaceae. Spore balls embedded in the host tissue of aquatic plants.			
Doassansia	1. Spore balls permanent, composed of spores surrounded by a cortex of sterile cells			
	 Spore balls loose, composed of a network of fine, branched hyphae in which the spores 			
Nannfeldtiomyces	are scattered, no cortex			
Geminago	On Sterculiaceae. Sori in hypertrophied flowers; spores in pairs, in cavities of host tissue			
Pericladium	On Tiliaceae (Malvaceae). Sori forming pustular galls on the twigs			
	On Trilliaceae (Liliaceae s. lat.). Spores in balls surrounded by sterile cells			
Entyloma	On Urticaceae. Spores solitary, hyaline, embedded in the host tissue			
	On Violaceae. Spores in balls surrounded by sterile cells			
On Vitaceae.				
Mvcosvrinx	1. Sori forming witches' brooms; spores in pairs, powdery			
Entvloma	- Sori forming leaf spots; spores single, embedded in the host tissue			

For **A tentative key to the genera of smut fungi**, based on selected characters and on host taxonomy, see Vánky 2008c:168-175, and for **Keys to smut fungi of selected host plant families and genera**, see Vánky 2009a:1-36.

GLOSSARY

abaxial: that surface of any structure which is remote or turned away from the axis

adaxial: that surface of any structure which is turned toward axis

allantoid: slightly curved with rounded ends; sausage-like in form

anamorph: the asexual (imperfect) form of a fungus

ballistoconidia, ballistospores: forcibly abjected propagules

basidiospore: spore produced on basidium

basidium (pl. -ia): the organ of basidiomycetes from which usually basidiospores are produced

blastic: one of the two basic sorts of conidiogenesis, characterized by a marked enlargement of a recognizable

conidial initial before the initial is delimited by a septum

blastoconidium: a blastic conidium

capillitium (elater): sterile, thread-like fungal elements between the spores

clavate: club-shaped

columella (pl. -ae): a central axis within a sorus (usually of fungal and host origin)

comb. nov.: combinatio nova: new combination comm., communico: share, divide, receive

conidiophore: a fertile hypha on which conidia are produced

conidium: a specialized, non-motile, asexual spore

cuneiform: wedge-shaped

dikaryon (adj. dikaryotic): a cell having two genetically distinct haploid nuclei

disjunctor: a connective cell or projection

elater (see capillitium)

emend. (emendatus, -a ,-um): used in author citation when an author has changed the circumscription of a taxon but has not excluded its type

epiphyllum: upper-, adaxial side of a leaf

haustorium (pl. -ia): an outgrowth of a hypha which serves to draw food from a host cell

holobasidium: a whole, aseptate basidium

homothallism (adj. homothallic): the condition in which sexual reproduction can occur without the interaction of two differing thalli

hypha (pl. -ae): one of the filaments of a mycelium

hypophyllum: under-, abaxial side of a leaf

karyogamy: union and interchange of nuclear material

muri: wall (used for the wall of the meshes of spore ornamentation)

mycelium: a mass of hyphae; the thallus of a fungus

nomenclatural synonym (homoytypic synonym): a synonym based on the same type as that of another name in the same rank

operculate: having a lid-like structure

operculum: lid, covering

parenchyma: plant tissue of parenchymatous cells

peridium: outer covering of a sorus phragmobasidium: a septate basidium

phylogeny: (history of) evolution of animal or plant type

pleurogenous or pleurogenic (conidia) = developed on the sides of a conidiophore

polycystic: having many, bladder-like structures

retraction septum: a cell wall formed when the cytoplasm is moving from one part of the fungus to another

saprobic, saprophytic: living on dead or decaying organic matter septal pore: the opening on a septal wall between two cells

soma: body

sorus (pl. sori): a fruiting structure or the place where the spores are produced

spicule, spinule = thorn, prickle

spore ball: an ephemeral or permanent agglomeration of spores with or without other fungal elements

sterigma (pl. -ata): an extension of the basidium on which basidiospores are produced

stroma (pl. -ata): a mass of vegetative hyphae

taxon (pl. taxa): a taxonomic group of any rank

taxonomic synonym (heterotypic synonym): a synonym based on a type different from that of the accepted name.

teleomorph: the sexual (perfect) form of a fungus

teliospore: a basidium-bearing organ

type (typus), nomenclatural type of a species: the specimen on which it was described and to which its name is permanently attached

- holotype: the (one) specimen on which the species was described
- isotype: a duplicate specimen of the holotype
- lectotype: a type designated later from the syntypes
- neotype: a specimen selected as type when all original material is missing
- paratype; any specimen other than the holotype on which the first description is based
- syntypes: specimens on which the original description is based when no holotype was named
- topotype: a specimen (of a species) from the same locality as the type (of that species, collected later)

unispecific (monotypic) genus: a genus which includes only a single species

DESCRIPTIONS AND ILLUSTRATIONS OF GENERA

In this book 104 genera are presented, of which 102 are basidiomycetous and two are ascomycetous. Three genera are doubtful. Only smut fungi which develop teliospores are included. Groups of subphylum Ustilaginomycotina which do not have teliospores (e.g. Microstromatales, Malasseziales, Exobasidiales) are omitted. On the other hand, members of the Microbotryales (Microbotryaceae, Ustilentylomataceae), despite being placed under the subphylum Pucciniomycotina in the new classificatory system, are treated in this book.

ABBREVIATIONS

al. = alii, aliae, alia = others nom. nov. = nomen novum = new name auct. = auctores, auctorum = authors, of authors nom. nov. illeg. = nomen novum illegitimum = new, illegitimate name c. = circa = aboutCo. = countynom. nud. = nomen nudum, a name published without description or diagnosis (invalid name) Di = dicotyledonous plant(s) emend. = emendatus = corrected, amended nom. rej. = nomen rejiciendum = rejected name HUV = Herbarium Ustilaginales Vánky non = notin litt. = in litteris = in a letter $n.v. = non \ vidi = not \ seen$ LM = light microscopy prop. = propositus, -a, -um = proposed L.S. = longitudinal section p.p. = pro parte = in partMA = malt agarq.e. = quid est = which isMo = monocotyledonous plant(s) SEM = scanning electron microscopy MYP = malt-yeast-peptone agar s. lat. = sensu lato = in a broad sense nec = also nots. str. = sensu stricto = in a narrow sense TEM = transmission electron microscopy nom. = nomen = namenom. cons. = nomen conservandum T.S. = transversal sectionUst. exs. = Ustilaginales exsiccata = conserved name nom. invalid. = nomen invalidum = not validly WA = water agarpublished name

Abbreviations of **authors** of scientific names of fungi generally follow Kirk & Ansell (1992). However, no abbreviation is applied when only two letters are saved (Hawksworth 1980:473, Principle 1), e.g. Holway not Holw., Kellerman, not Kellerm., Mundkur, not Mundk., J. Schröter, not J. Schröt., Sydow, not Syd., or Thümen, not Thüm., etc. Likewise, no abbreviation is used when the name is followed by indication of literature. Furthermore, for several reasons, I prefer to use also the initial(s) of forename(s) for **all** the authors when several authors have the same surname. For example H. Sydow, P. Sydow, or in combination H. & P. Sydow, instead of Syd. & P. Syd. (Kirk & Ansell 1992:82), or H. Sydow & Sydow (as recommended by Hawksworth 1980:480). For the description of genera of smut fungi, the initials of the author's first name(s) are also presented.

Abbreviations of **herbaria** follow Index Herbariorum (Stafleu *et al.* 1981). HUV = Herbarium Ustilaginales Vánky (the author's private herbarium).

Abbreviations of **journals** follow BPH-2. Periodicals with botanical content. Compiler G.D.R. Bridson, 2004, Vol. 1-2.

Bars of drawings represent 1 cm, those of microphotos, spore germination, etc. 10 μ m, unless otherwise given.

1. AHMADIAGO K. Vánky, Mycotaxon 89:102, 2004d.

Sori on host plants in Euphorbiaceae (seeds), peridium, columella and sterile cells lacking. Spore mass dark brown, agglutinated to powdery. Spores single, pigmented (brown, without violet or orange-yellow tint). Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Type of the genus: A. euphorbiae.

Ahmadiago is currently a unispecific genus in the Ustilaginales.

Ahmadiago euphorbiae (B.B. Mundkur) K. Vánky,

Mycotaxon 89:103, 2004d.

Ustilago euphorbiae Mundkur, *Trans. Brit. Mycol. Soc. 24*:331, 1940. — Type on *Euphorbia dracunculoides*, India, Punjab, Kalashah Kaku, 18.VIII.1936, leg. S. Ahmad, HCIO; isotypes in IMI, K, HUV 5475!

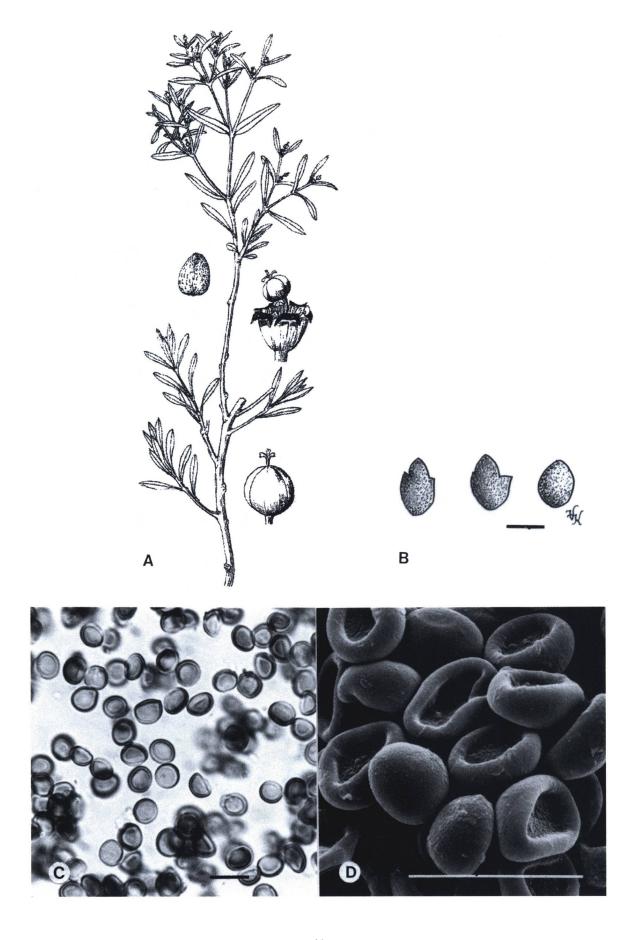
Sori (Fig. 1 B) in the seeds forming ovoid or slightly irregular, c. 2×3 mm large bodies with dark chocolate brown, agglutinated to powdery spore masses produced within the tissues of the endosperm, cotyledons and embryo, enclosed by the intact testa. True peridium and columella lacking. Spores (Figs. 1 C, D) globose, subglobose, ovoid, broadly ellipsoidal or slightly irregular with a more or less flattened side, 5-7(-8) \times 5.5-8(-9) μ m, olivaceous brown, paler on the flattened side; wall uneven, 0.7-0.8 μ m thick on the darker side, c. 0.2-0.3 thick on the paler side, smooth. Sterile cells absent. Spore germination unknown.

On Euphorbiaceae: Euphorbia dracunculoides Lam.; Asia. Known only from the type collection.

Ref.: Mundkur 1940, Vánky 2004d.

Fig. 1 A-D. Ahmadiago euphorbiae on Euphorbia dracunculoides, isotype, HUV 5475.

- **A.** A healthy plant of *Euphorbia dracunculoides* (Reproduced from the Flora of China, internet).
- **B.** Three infected, swollen and deformed seeds (Bar = 3 mm).
- C, D. Spores in LM and in SEM.



2. *AIZOAGO* K. Vánky, in Vánky & Shivas, *Mycobiota 1*:2, 2013.

Sori on vegetative parts and fruits of plants in Aizoaceae, bullate, filled with a dark, semiagglutinated mass of spores. Columella and sterile cells absent. *Spores* solitary, pigmented (yellowish brown, no violet or reddish tint), ornamented and covered by a thick sheath, formed in septate sporogenous hyphae.

Aizoago has two species, known from Australia: A. tetragonioides Vánky & R.G. Shivas, on Tetragonia tetragonioides (Pallas) Kuntze, and the type of the genus:

Aizoago tetragoniae K. Vánky & R.G. Shivas Mycobiota 1:3, 2013.

Type on *Tetragonia diptera* F. Muell., Australia, Western Australia, Shark Bay, 1971, leg. H.L. Harwey. Holotype IMI 162907, isotypi DAR 59828, HUV 21961!

Sori (Fig. 2 A) on the stems and fruits producing bullate swellings up to 1 cm in diameter, first covered by host tissue that ruptures at maturity, exposing the dark reddish brown, semiagglutinated mass of spores. Columella and sterile cells absent. Spores (Figs 2 C, D) globose, subglobose, ellipsoidal to slightly irregular, 22.5-30 × 24-36 μm (including the sheath). The proper spores are globose to ellipsoidal, 16-23 μm long, yellowish brown with an evenly 0.5-0.8 μm thick wall that is indistinctly, completely or usually incompletely reticulate and often also sparsely verruculose. Muri on the spore circumference thin, acute, 1.5-4 μm high, 17-28 on the spore circumference. The sheaths are evenly or unevenly 3-11 μm thick, pale yellowish brown, composed of a slightly darker inner layer, into which the muri penetrate, and 1-3 paler outer layers. Spore formation (Fig. 2 B) in septate sporogenous hyphae, in rows or rarely in groups. Immature spores globoid, rounded subpolyhedrally irregular, rarely elongate or lacrymiform, at beginning lacking sheath, having only a thin, hyaline spore wall which gradually becomes pigmented and finally ornamented and with a thick, subhyaline sheath.

On Aizoaceae: Tetragonia diptera F. Muell., Australia. Known only from the type locality.

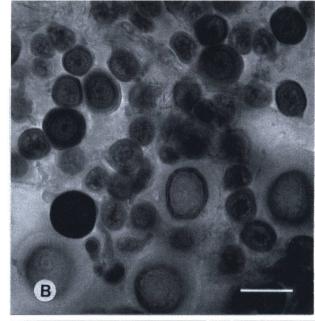
Ref.: Vánky & Shivas 2013.

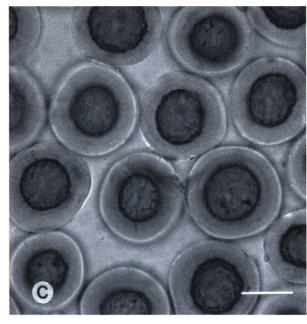
Fig. 2 A-D. Aizoago tetragoniae on Tetragonia diptera, isotype, HUV 21961.

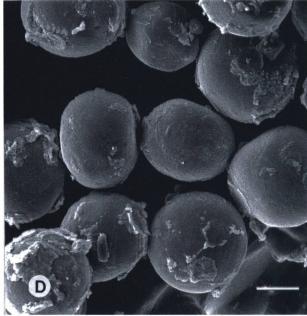
- A. Sori on a pedicel and in a fruit. Habit (Bar = 1 cm).
- **B.** Spore formation in sporogenous hyphae, in LM (Bar = $10 \mu m$).
- **C-D.** Mature spores in LM and in SEM (Bars = $10 \mu m$).



Α







3. ANOMALOMYCES K. Vánky, M. Lutz & R.G. Shivas, Mycol. Balcan. 3:120, 2006. emend. Vánky & R.G. Shivas, in Shivas, Lutz, McTaggart & Vánky, Mycobiota 1:22. 2013.

Sori in hypertrophied ovaries of Poaceae divided into compartments by membranes of host tissue permeated by hyphae, peridium of host and fugal tissue present, columella absent. Spores pigmented (brown, without violet or reddish tint), forming permanent spore balls. Outermost spores in the balls covered by a hard, darkly pigmented, amorphous cortex, formed by agglutinated, strongly modified fungal cells. Spore balls permanent, composed of pigmented (brown) spores, coated by the cortex. Sterile cells between the spore balls variable in morphology and frequency, of one or more types. Spore germination results in phragmobasidia producing basidiospores laterally and terminally.

Anomalomyces, belonging to the Ustilaginaceae, has two species: A. yakirrae R.G. Shivas, M. Lutz, A.R. McTaggart & Vánky on Yakirra pauciflora, and the type of the genus:

Anomalomyces panici K. Vánky, R.G. Shivas & M. Lutz in Vánky, Lutz & Shivas, Mycol. Balcan. 3:120, 2006.

Type on *Panicum trachyrhachis*, Australia, Northern Territory, 100 km S of Darwin, Snake Creek, alt. 140 m, 9.VI.2006, leg. M.J. Ryley, M.D.E. & R.G. Shivas, BRIP 47952; isotype HUV 21366!

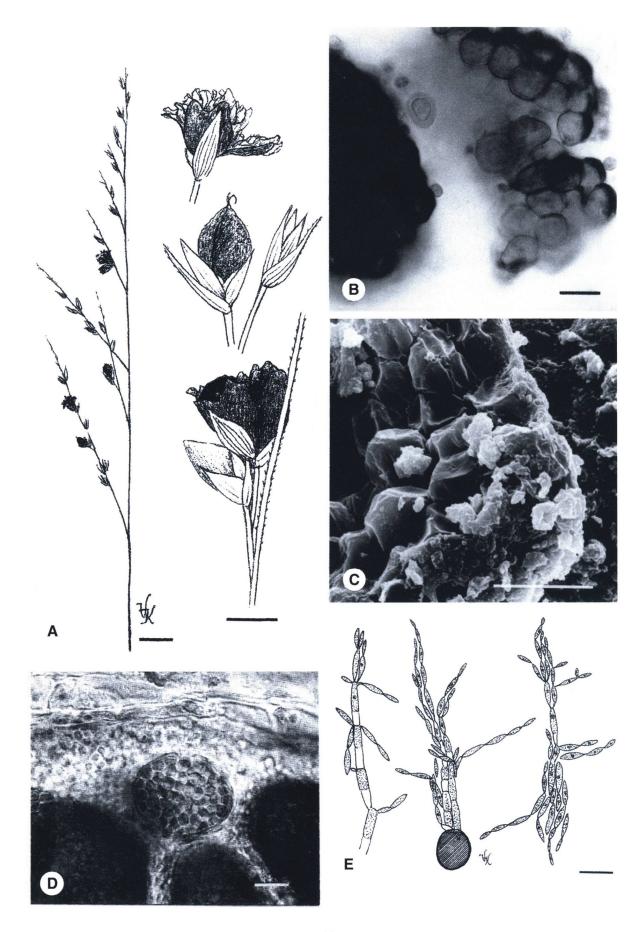
Sori (Fig. 3 A) in some ovaries of an inflorescence, globoid or ovoid, 1.5-3 × 2-3.5 mm, covered by a thick peridium of host and fungal origin, initially green, becoming brown, at maturity rupturing irregularly at the apex, exposing the dark brown, semi-agglutinated to granular-powdery mass of spore balls mixed with numerous sterile cells. Columella lacking but the sori are divided into incomplete and irregular compartments by membranes of host tissue permeated by hyphae. In the hyaline mass of sporogenous hyphae agglomerated groups of elongate spore initials appear, each with a rounded top. These increase in size, become globoid, 4-5 μm in diameter. During this early stage the spore balls become delimited by a 2-2.5 μm thick, olive-brown, continuous layer formed of the thickened external wall of the outermost spores. During maturation, the spores increase in size, become pigmented and polyangular by mutual pressure whereas the hyaline fungal mass around the spores and the spore balls is gradually consumed, excepting some fungal cells from which sterile cells develop. Spore balls (Figs. 3 B, C) subglobose, ovoid, ellipsoidal to subpolyhedrally irregular, 25-120 × 30-200 μm, dark olive-brown or opaque, permanent, composed of tens to hundreds of tightly packed spores that separate by strong pressure. Spores (Figs. 3 B, C) rounded subpolyhedrally or polyhedrally irregular, 8-10.5 × 8-11(-12) μm, pale olive-brown; wall even, thin (c. 0.5 μm), smooth, except for the free surface of the outermost spores in the balls which is 1-2.5 µm thick, dark olive-brown, apparently smooth to very finely punctate-verruculose, in SEM two or several rounded, low warts often fusing and forming an irregular pattern. Sterile cells (Figs. 3 B, C) between the spore balls of two types, one large and one small, both solitary. Sterile cells of the larger type globose, subglobose, ovoid, ellipsoidal or slightly irregular, 7-12 × 8-15 µm, pale olive-brown; wall of two layers, even or slightly uneven, 1.2-2.5 µm thick, smooth. Sterile cells of the smaller type globose, subglobose, ovoid, rounded subpolyhedrally irregular, often with one or two subacute tips, then tear- or lemon-shaped, 2.5-5 × 3-5.5 µm, medium dark olive-brown; wall thin (c. 0.2-0.3 µm), smooth, often with a narrow, short hyphal appendage, up to 5 μm long. Spore germination (Fig. 3 D) results in 4-6-celled phragmobasidia, 2.5 × 30-60 μm. Basidiospores numerous, fusiform, produced laterally and terminally on sterigmata on the basidia, $0.8-1.5 \times 8-13$ μm, giving rise by germination to a chain of successively smaller, fusiform sporidia.

On Poaceae: Panicum trachyrhachis Benth.; Australia.

Ref.: Vánky, Lutz & Shivas 2006, Shivas, Lutz, McTaggart & Vánky 2013.

Fig. 3 A-D. Anomalomyces panici on Panicum trachyrhachis, isotype, HUV 21366.

- **A.** Sori in some ovaries. Habit and enlarged three sori and some healthy spikelets (Bars = 1 cm).
- **B-C.** Spore balls, spores and sterile cells in LM and in SEM (Bars = $10 \mu m$).
- **D.** Section of a young sorus with developing spore balls (in lactophenol with cotton blue; Bar = $10 \mu m$).
- **E.** Germinating spores (in water, at room temp., in one day; Bar = $10 \mu m$).



4. *ANTHEROSPORA* R. Bauer, M. Lutz, D. Begerow, M. Piątek & K. Vánky, in Bauer, Lutz, Begerow, Piątek, Vánky, Bacigálová & Oberwinkler, *Mycol. Res. 112*:1300, 2008.

Sori in the flowers (usually in the anthers, but also on filaments, gynoeceum or in the ovaries) of host plants in Hyacinthaceae (Liliaceae s. lat.), lacking peridium and columella. Spore mass blackish brown, powdery. Infection systemic, all flowers of an inflorescence affected. Spores single, pigmented (yellowish brown, without violet tint, orange or rusty color). Sterile cells absent. Spore germination results in phragmobasidia. Host-parasite interaction by haustoria. Septal pore simple, with two membrane caps and two non-membranous plates closing the pore. Type of the genus: A. vaillantii.

Antherospora has eight known species in the Floromycetaceae, order Urocystidales.

Antherospora vaillantii (Tul. & C. Tul.) R. Bauer, M. Lutz, D. Begerow, M. Piątek & K. Vánky, in Bauer, Lutz, Begerow, Piątek, Vánky, Bacigálová & Oberwinkler, Mycol. Res. 112:1304, 2008.

Ustilago vaillantii Tul. & C. Tulasne, Ann. Sci. Nat. Bot., Sér. 3, 7:90, 1847. — Yenia vaillantii (Tul. & C. Tul.) Liou, Contr. Inst. Bot. Natl. Acad. Peiping 6:45, 1949. — Vankya vaillantii (Tul. & C. Tul.) Ershad, Rostaniha 1:69, 2000.— Lectotype (design. by Lindeberg 1959:141) on Muscari comosum, France, leg. S. Vaillant, PC.

Ustilago vaillantii forma muscari Rabenhorst, Hedwigia 15:109, 1876 (nom. nud.). — On Muscari comosum, Czech Rep., near Brünn [Brno], V-VI.1875, leg. G. Niessl; in Rbh., Fgi. eur. no. 2097, HUV 4900!

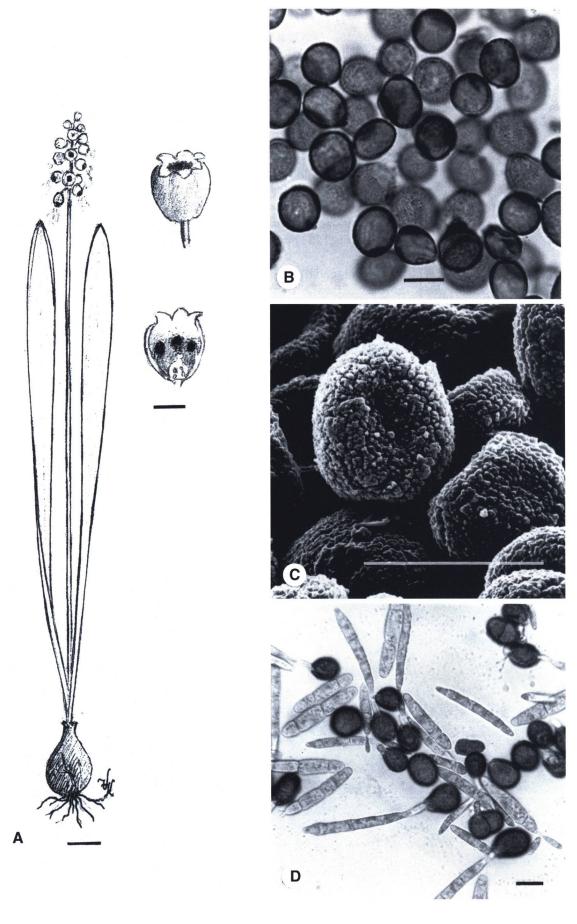
Ustilago muscari-botryoidis Ciferri, Ann. Mycol. 26:14, 1928. — Type on Muscari botryoides, Italy, Piemonte, Cuneo Prov., Alba Distr., Moretta, "verso Santa Rosalia", 1921, leg. R. Ciferri. Type not found (Syn. by Vánky 1985a:249).

Sori (Fig. 4 A) in all, slightly swollen flowers of an inflorescence, in the anthers and on the filaments, rarely also on the gynoecium and in the ovaries, filling the flowers with a dark olive-brown, powdery mass of spores. Infection systemic. Distal, sterile flowers of an infected inflorescence develop anthers producing spores. *Spores* (Figs. 4 B, C) varying in shape and size, globose, subglobose, ovoid, curved, pyriform, tear-shaped, or irregularly elongate, 6-8(-9) × (6-)6.5-10.5(-11.5) μm, olive-brown; wall even, c. 0.5 μm thick, finely, densely verruculose, spore profile finely wavy, in SEM densely and irregularly verruculose-tuberculate, tubercles often irregularly fused. *Spore germination* (Fig. 4 D; J. Schröter, in Cohn 1877a:358, Pl. XII, fig. 4; Ingold 1984:251, fig. 3) results in 4-celled basidia (usually the uppermost three-celled part separating from the basal cell) producing laterally and terminally elongate, sessile, budding basidiospores, or basidiospores develop on short sterigmata.

On Hyacinthaceae (Liliaceae s. lat.): *Muscari alpinum* J. Gay (cult.), *M. botryoides* (L.) Mill., *M. comosum* (L.) Mill. (*Leopoldia comosa* (L.) Parl.; *M. tubiflorum* Steven), *M. moschatum* Willd. (*Muscarimia muscari* (L.) Losinsk.), *M. neglectum* Guss. ex Ten. (*M. racemosum* (L.) Lam. & DC.), *M. schliemanni* Freyn & Asch. (cult.), *M. tenuiflorum* Tausch (*Leopoldia tenuiflora* (Tausch) Heldr.); Europe, Africa, Asia, N America.

Ref.: Bauer, Lutz, Begerow, Piatek, Vánky, Bacigálová & Oberwinkler 2008.

- **Fig. 4 A, D.** *Antherospora vaillantii* on *Muscari botryoides*, Vánky, Ust. exs. no. 899 (as *Ustilago vaillantii*), HUV 15686.
- A. Sori in all flowers of an inflorescence. Habit (Bar = 1 cm), and enlarged two infected flowers, one opened, showing the spore masses in the anthers (Bar = 2.5 mm).
- **B, C.** Antherospora vaillantii on *M.* comosum, Vánky, Ust. exs. no. 88 (as *Ustilago vaillantii*), HUV 4923. Spores in LM and in SEM.
- **D.** Spore germination (on MYP, at room temp., in one day; Bars = $10 \mu m$).



5. ANTHRACOCYSTIS O. Brefeld.

Unters. Gesammtgeb. Mykol. 15:53, 1912, emend. McTaggart & R.G. Shivas, in McTaggart, Shivas, Geering, Vánky & Scharaschkin, Persoonia 29:119, 2012c.

LUNDQUISTIA Vánky, Mycotaxon 77:371, 2001, emend. Vánky, Fungal Diversity 17:160, 2004. — Type: L. fascicularis Vánky on Digitaria brownii (Roem. & Schult.) Hughes, Australia, New South Wales, NW of Hermidale, between Cobar and Nyngan, 1.III.1971, D.A. Campbell, DAR 58832, HUV 19444.

Sori replacing inflorescences, all of the racemes or localised in spikelets of an inflorescence. Peridium of vacuolated fungal cells surrounded by host cells. Columella composed of vascular bundles surrounded by host parenchyma permeated by inter- and intracellular hyphae, often separated into several columellae each around a vascular bundle surrounded by parenchyma, filiform, flexuous, flattened. Sporogenous hyphae coiled or unknown. Spores compacted in spore balls, globose to subglobose, often outer spores darker than inner spores. Sterile cells few or absent. The genus comprises 126 species. Type of the genus:

Anthracocystis destruens (D.F.L. Schlechtendal) O. Brefeld, Unters. Gesammtgeb. Mykol. 15:53, 1912.

Caeoma destruens Schlechtendal, Fl. Berol., Pars 2. Cryptogamia:130, 1824. — Uredo destruens (Schltdl.) Duby, Botanicon Gallicum, Ed. 2, Pars 2:901, 1830. — Tilletia destruens (Schltdl.) Léveillé, Ann. Sci. Nat. Bot., Sér. 3, 8:372, 1847. — Ustilago destruens (Schltdl.) Rabenhorst, Herb. viv. myc., ed. 2, no. 400, 1857. — Sphacelotheca destruens (Schltdl.) J.A. Stevenson & A.G. Johnson, Phytopathology 34:613, 1944. — Sporisorium destruens (Schltdl.) Vánky, Symb. Bot. Upsal. 24(2):115, 1985. — Neotype (design. by Vánky 1985:116) on Panicum miliaceum, Germany, Bunzlau [Poland, Bolesławiec], J. Kühn, HUV 1895!; isoneotypes in Rbh., Herb. viv. myc., ed. 2, no. 400 (as 'Ustilago destruens'). The holotype was lost in Berlin during World War II. No isotypes are preserved in Herb. Schlechtendal (HAL) either.

Uredo segetum Pers. δ Uredo Panici-miliacei Persoon, Syn. meth. fung. 1:224, 1801. — Uredo carbo δ panici-miliacei (Pers.) de Candolle, Fl. franç., ed. 3, 6:76, 1815. — Erysibe panicorum β panici-miliacei (Pers.) Wallroth, Flora Cryptogamica Germaniae 2:216, 1833. — Ustilago panici-miliacei (Pers.) G. Winter, Rabenh. Krypt.-Fl., 2 Aufl., 1(1):89, 1881. — Sorosporium panici-miliacei (Pers.) Takahashi, Bot. Mag. (Tokyo) 16:184 & 247, 1902. — Sphacelotheca panici-miliacei (Pers.) Bubák, Houby Ceské 2:27, 1912. — Type on Panicum miliaceum, sine loco (Syn. by McAlpine 1910:201).

Sorosporium manchuricum S. Ito, Trans. Sapporo Nat. Hist. Soc. 14:93, 1935. — Sphacelotheca manchurica (S. Ito) Y.C. Wang, Acta Bot. Sinica 10:134, 1962. — Type on Panicum miliaceum, Japan, Hokkaido, Ishikari Prov., Sapporo, 5.IX.1910, S. Hashimoto; isotype HUV 20649! (Syn. by Ling 1953:329).

Sphacelotheca lioui W.Y. Yen, Contr. Inst. Bot. Natl. Acad. Peiping 4:193, 1937. — Type on Panicum miliaceum, China, Shan-si [= Shanxi] Prov., Ta-tung, 6.VIII.1934, T.N. Liou (Syn. by Ling 1953:329).

Sori (Fig. 5 A) destroying the whole inflorescence, ovoid to elongate, 0.5-2 × 3-6 cm, partly concealed by leaf sheaths and covered by a well-developed, whitish peridium that ruptures irregularly and flakes away to expose the dark brown, dusty spore mass, sterile cells and numerous, long, filiform columellae composed of host tissues, mainly vascular bundles, and hyphae. Infection systemic, initiated in seedling stage of the hosts. *Spore balls* (Figs 5 B) loose, ephemeral. *Spores* (Figs 5 B, C) when mature single, subglobose, ovoid to elongate or irregular, 7-9 × 8-13 μm, pale reddish brown; wall even or nearly so, c. 0.5 μm thick, smooth to very finely punctate, spore profile smooth, in SEM very finely and densely verruculose. *Sterile cells* between the spores subhyaline or pale yellow, thin-walled, almost the size of the spores. *Spore germination* (Fig. 5 D; Brefeld 1883:97-101; Vasey 1918:11) results in 4-celled basidia. In water, basidial cells fuse and produce hyphae, in nutrient media abundant basidiospores are produced.

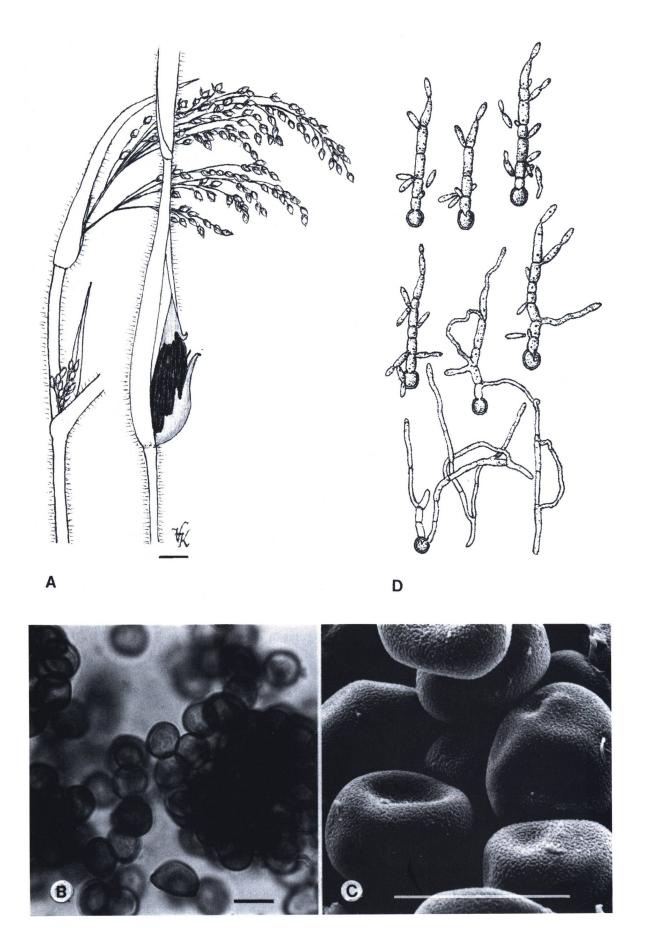
On Poaceae: Panicum capillare L., P. miliaceum L. (cult.); cosmopolitan.

For the nomenclature of this fungus see Stevenson & Johnson 1944:613. The reported few sterile cells in *Anthracocystis destruens* (Vánky 1994b) are most likely remnants of non-sporogenous hyphae.

Ref.: Brefeld 1883, 1912, McTaggart, Shivas, Geering, Vánky & Scharaschkin 2012c

Fig. 5 A-D. Anthracocystis destruens on Panicum miliaceum (cult.).

- **A.** A sorus destroying the whole inflorescence, partly enclosed by a leaf sheath and covered by the rupturing peridium. To the left a healthy panicle (Bar = 1 cm).
- **B.** C. A spore ball and spores in LM and in SEM (Bars = $10 \mu m$).
- **D.** Spore germination in nutrient media (After Brefeld 1883).



6. ANTHRACOIDEA O. Brefeld,

Unters. Gesammtgeb. Mykol. 12:144, 1895.

CINTRACTIA Cornu, sensu ampl. Magnus (1896('1895'):78) et auct. plur., p.p., non Cintractia Cornu (1883:279) s. str. orig.

CINTRACTIOMYXA Golovin, Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Komarova Akad. Nauk SSSR 8:108, 1952. — Type: C. caricis Golovin (= Anthracoidea externa (Griffiths) Kukkonen) on Carex pachystylis J. Gay (= C. stenophylla Wahlenb.), Kazakhstan, Kampyr-Darbasa, near Kabulsay, 3.V.1924, leg. E.A. Mokeeva. (Syn. by Nannfeldt & Lindeberg 1957:503).

Sori in and around ovaries of plants in Cyperaceae, globose to oblong-ovoid, composed of the nutlets surrounded by a black, firmly agglutinated spore mass, originally covered by a thin, grayish or silvery fungal membrane. Spores single, pigmented (dark brown), globose, ovoid to more or less irregular, subpolyhedral, often flattened, relatively large (average length 13-31 µm). Spore wall usually ornamented (with spines, warts or granules), rarely smooth, often with internal swellings or light-refractive areas. Spore germination results in two-celled basidium forming one or more basidiospores on each cell. Anamorph (Crotalia Liro) present in some species. Host-parasite interaction (Fig. 7, p. 24) by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Type of the genus: A. caricis.

Anthracoidea, in the Anthracoideaceae, with ca. one hundred known species, forms a natural group, parasitizing members of Cyperaceae: Carex, Carpha, Fuirena, Kobresia, Schoenus, Scirpus (Trichophorum) and Uncinia. It is divided into two subgenera: Anthracoidea and Proceres Kukkonen, based on the type of spore germination (see Fig. 4 F a, b).

Anthracoidea caricis (C.H. Persoon) O. Brefeld,

Unters. Gesammtgeb. Mykol. 12:144, 1895 (as "*Carycis*"), emend. Nannfeldt, *Symb. Bot. Upsal. 22(3)*:17, 1979.

Uredo caricis Persoon, Syn. meth. fung. 1:225, 1801. — Caeoma caricis (Pers.) Link, in Willdenow, Linné's Species Plantarum Ed. 4, 6(2):5, 1825. — Ustilago caricis (Pers.) Unger, Ueber den Einfluß des Bodens, etc.:211, 1836. — Cintractia caricis (Pers.) Magnus, Verh. Bot. Vereins Prov. Brandenburg 37:79, 1896('1895'). — Neotype (design. by Kukkonen 1963:58) on Carex pilulifera L., Germany, Brandenburg, Kreis Zauch-Belzig, between Beelitz and Schlunkendorf, 10.VI.1935, leg. E. Fahrendorff, TUR; isoneotypes in Sydow, Mycoth. germ. no. 2880 (as Cintractia caricis), HUV 143!

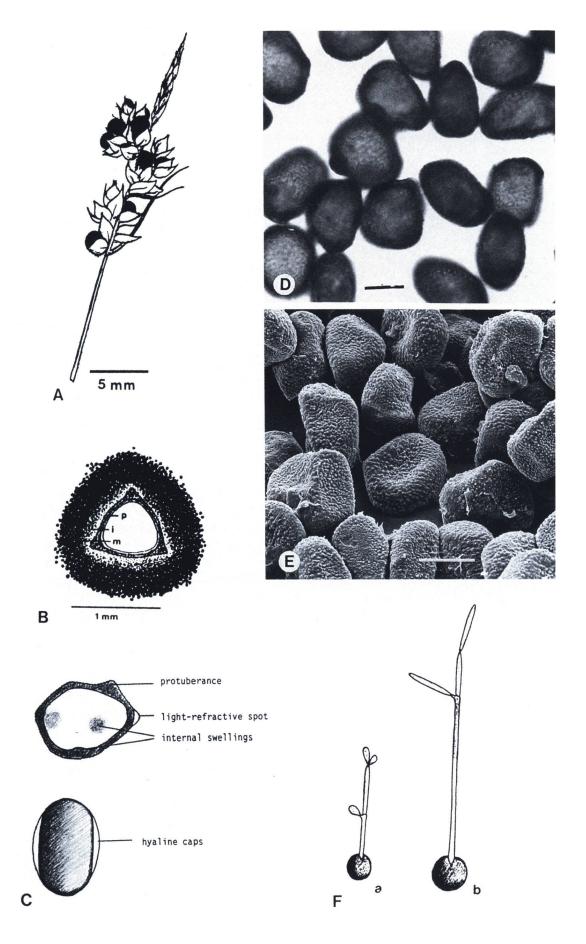
Uredo urceolorum De Candolle, Fl. franç., ed. 3, 6:78, 1815, nom. nov. superfl. pro Uredo caricis Pers.

Sori (Figs. 6 A, B) in single ovaries forming globose, black, hard bodies, 1-2 mm in diameter, initially covered by a thin, grayish membrane, later black, powdery on the surface. Spores (Figs. 6 D, E) medium-sized, flattened (11-15 μm thick), in plane view subcircular, angular or irregular, 14-20(-22) x 15-25(-28) μm, reddish brown; wall of uneven thickness, 1-3(-4) μm, thickest at the angles, 1-3 indistinct internal swellings may be present, light-refractive areas uncommon or lacking; surface evidently verrucose, spore profile wavy or finely serrulate, in SEM covered with more or less regularly and densely situated, low, rounded warts, c. 0.3-0.6 μm in diameter, between them minute, densely situated papillae are seen. Spore germination of Anthracoidea-type.

On Cyperaceae: Carex (subgen. Carex, sect. Acrocystis = Montanae) species; Europe, Asia, N America.

Ref.: Liro 1938, Lehtola 1940, Savile 1952, Nannfeldt & Lindeberg 1957, 1965, Tomková-Soucková 1960, Kukkonen 1961, 1963, 1964a, 1964b, 1965, 1969, Boidol & Poelt 1963, Kukkonen & Raudaskoski 1964, Kukkonen & Vatanen 1968, Nannfeldt 1977, 1979, Zambettakis 1978, Braun & Hirsch 1978, Kukkonen & Timonen 1979, Vánky 1979, Karatygin 1982, Azbukina & Khavkina 1984, Ingold 1989, Denchev 1991, 1997., Salo & Sen 1993, Guo 1994, Hendrichs 2004, Hendrichs, Begerow, Bauer & Oberwinkler 2005.

Fig. 6 A, C-E. Anthracoidea caricis on Carex pilulifera L., isoneotype, Sydow, Mycoth. march. no. 2880, HUV 143. **A.** Sori in some ovaries as black, hard, globoid bodies. **B.** T.S. of a sorus of A. carphae (Speg.) Vánky, p = pericarp, i = immature, m = mature spores. **C.** Spores schematically. **D.** Spores in LM and **E.** in SEM. **F.** Subgen. Anthracoidea (a), and subgen. Procees (b) type of spore germination.



7. AURANTIOSPORIUM M. Piepenbring, K. Vánky & F. Oberwinkler, Pl. Syst. Evol. 199:62, 1996, emend. Vánky, Mycotaxon 70:18, 1999a.

Sori in spikelets of Cyperaceae producing hypertrophy. Spore mass orange-yellow to rusty brown, granular-powdery, composed of loose or permanent spore balls. Spores more or less irregular, pigmented (yellow to yellowish red). Spore wall usually of irregular thickness, multilayered. Spore germination results in phragmobasidia bearing sessile basidiospores. Host-parasite interaction by intercellular hyphae lacking interactions with deposits of specific fungal vesicles. Septal pore simple, lacking caps.

Aurantiosporium, in the Ustilentylomataceae, Microbotryales, has four known species: **1.** A. marisci Vánky & C. Vánky on Mariscus thunbergii (Vahl) Schrad., South Africa, **2.** A. pallidum M. Piepenbr. on Scleria bracteata Cav., Bolivia, **3.** A. scleriae Vánky on Scleria flexuosa Böckeler, Malawi, and **4.** The type of the genus:

Aurantiosporium subnitens (J. Schröter & P. Hennings) M. Piepenbring, K. Vánky & F. Oberwinkler, Pl. Syst. Evol. 199:62, 1996.

Ustilago subnitens J. Schröter & Henn., in Hennings, Hedwigia 35:215, 1896. — Cintractia subnitens (J. Schröter & Henn.) Castellani & Ciferri, Prodromus mycoflorae Africae Orientalis Italicae. Firenze:29, 1937 (n.v.). — Type on Scleria pratensis (= S. melaleuca), Brazil, State Rio de Janeiro, V.1887, leg. E. Ule 1604, HBG.

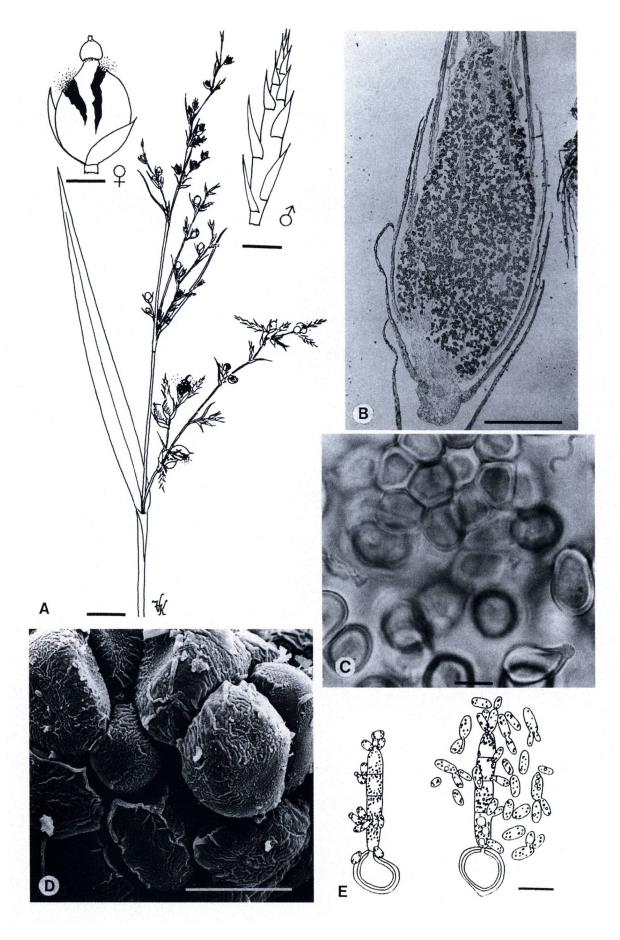
Aurantiosporium colombianum M. Piepenbring, Caldasia 24:105, 2002. — Type on Scleria lagoensis, Colombia, Magdalena Div., Santa Marta, 1898-1899, leg. Smith 237, COL; isotype BPI 840957. (Syn. by Vánky 2004d:111).

Sori (Figs. 7 A, B) in some of the male and female spikelets of an inflorescence forming elongate or ovoid galls, $2\text{-}4 \times 4\text{-}9$ mm, filled with orange colored to cinnamon brown mass of spore balls and spores. Sori at maturity crumbling into pieces. Spore balls (Figs. 7 C, D) subglobose, elongate to irregular, $30\text{-}70 \times 50\text{-}110 \,\mu\text{m}$, orange-yellow, easily separating into single spores. Spores (Figs. 7 C, D) subglobose, ovoid to subpolyhedrally irregular, $(8\text{-})10\text{-}12(\text{-}13) \times (10\text{-})13\text{-}17(\text{-}19) \,\mu\text{m}$, lemon- to orange-yellow; wall in LM smooth, two-layered, the outer layer usually irregularly (1-)1.5-2.5(-3) μ m thick, thickest at the angles, in TEM with numerous layers, in SEM with an irregularly folded surface, the dried, thin, gelatinous sheath. Spore germination (Fig. 7 E) results in 4-celled basidia of c. $5 \times 30 \,\mu$ m on which numerous, sessile, ovoid basidiospores are produced successively, c. $2 \times 3\text{-}6 \,\mu\text{m}$. On culture media basidiospores bud giving rise to yeast colonies.

On Cyperaceae: *Scleria lagoensis* Boeck., *S. melaleuca* Reichb. ex Schltdl. & Cham. (*S. pratensis* Lindl. ex Nees), *S. schimperiana* Boeck.; Africa (Ethiopia), C & S America.

Ref.: Hennings 1896, Piepenbring, Vánky & Oberwinkler 1996, Vánky 1999a.

- Fig. 7 A-E. Aurantiosporium subnitens on Scleria melaleuca, Vánky, Ust. exs. no. 896 (as Ustilago subnitens), HUV 15683.
- **A.** Sori in some spikelets in the inflorescence. Habit and enlarged two sori, one in a female spikelet, the other in a male spikelet (Bar for habit = 1 cm, for detail drawings = 2 mm).
- **B.** L.S. of a sorus in a male spikelet with spore balls and spores between the host cells (Bar = 0.5 mm).
- C, D. Spore balls and spores in LM and in SEM (Bars = $10 \mu m$).
- **E.** Spore germination (on WA, at room temp., after 1-3 days) results in septate basidia on which, laterally and terminally, numerous, sessile, ovoid basidiospores are produced (Piepenbring, Vánky & Oberwinkler 1996:59; Bar = $10 \mu m$).



8. BAMBUSIOMYCES K. Vánky,

Mycol. Balcan. 8:141, 2011.

Sori on the surface of host plants in the tribe Bambuseae (fam. Poaceae), dark brown, powdery, composed of spores only, no sterile cells. *Spores* single, pigmented (brown, without violet or red tint). *Spore germination* results in a short holobasidium producing apically ovoid or ellipsoidal basidiospores. It is a monospecific genus. *Type of the genus:*

Bambusiomyces shiraianus (Henn.) Vánky,

Mycol. Balcan. 8:142, 2011.

Ustilago shiraiana Hennings, Bot. Jahrb. Syst. 28: 260, 1901. — Type on Bambusa veitchii Carrière (= Sasa veitchii (Carrière), Japan, Nikko, Yumoto, VI.1899, Shirai, TNS; isotypes HBG, HUV 16635!

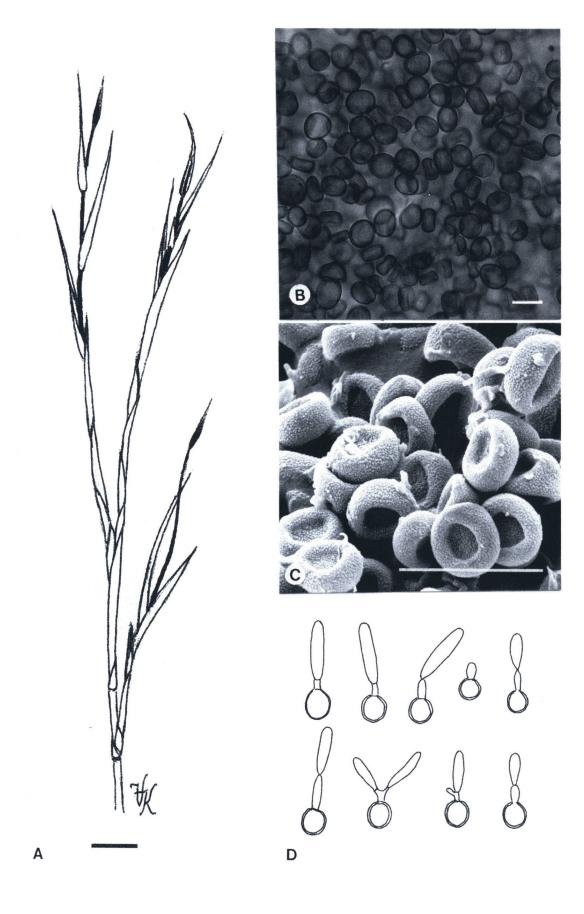
Sori (Fig. 8 A) surrounding the stems of shortened internodes of the young end-branches, partly concealed by leaf sheaths. Sori also on both surfaces of the proximal part of the leaf sheaths as small striae between the veins but by confluence may cover larger parts of the distal leaf sheaths and, at the top of the shoots, comprising also the small, congested leaves. Spore mass blackish brown, semiagglutinated to powdery, produced on the surface of the host tissues. The fungus often produces witches' broom. *Spores* (Figs 8 B, C). globoid, flattened, 4-5.5 μm wide, in face view circular or subcircular, rarely ovoid or elliptic, 5.5-7 x 6.5-8(-9) μm, pale yellowish brown; wall even, c. 0.5 μm thick, smooth, in SEM finely, densely verruculose. *Spore germination* (Fig. 8 D; Hino 1961: 228) results in a short, simple, rarely apically bifurcate, aseptate basidium, 3–5 x 15–20 μm, apically producing ovoid or ellipsoidal basidiospores measuring 2.5–4 x 3–9 μm.

On Poaceae: Arundinaria, Bambusa, Indocalamus, Phyllostachys, Pleioblastus, Sasa, Sasaella, Sasamorpha and Semiarundinaria species; S and E Asia, N America.

Ref.: Hennings 1901, Hino 1961, Vánky 2011a.

Fig. 8 A-C. Bambusiomyces shiraianus on Sasa veitchii (type).

- A. Sori on the surface of the internodes and apical leaves of young shoots. Habit (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM. (Bars = $10 \mu m$).
- **D.** Germinating spores of *Bambusiomyces shiraianus* (After Hino 1961: 228, fig. 134).



9. BAUERAGO K. Vánky, Mycotaxon 70:44, 1999.

Sori in seeds of monocotyledonous host plants (Commelinaceae, Cyperaceae and Juncaceae), peridium and columellae absent, spore mass powdery. Spores solitary, yellow to rusty brown pigmented, lacking violet tint. Sterile cells lacking between the spores. Spore germination results in phragmobasidia with sessile basidiospores. Host-parasite interaction by intercellular hyphae lacking interactions with deposits of specific fungal vesicles. Septal pore simple, lacking caps. Anamorph may be present.

Bauerago, in the Ustilentylomataceae, Microbotryales, has nine known species: 1. B. boliviana M. Piepenbr. on Commelina sp., from Bolivia, 2. B. capensis (Reess) Vánky on Juncus capensis, from S Africa, 3. B. combensis (Vánky) Denchev on Commelina benghalensis, from Pakistan, 4. B. commelinae (Kom.) Denchev on Commelina communis, from E Asia and N America, 5. B. cyperi-lucidi (J. Walker) Vánky on Cyperus lucidus, from Australia, 6. B. gardneri (McKenzie & Vánky) Vánky on Cyperus ustulatus, from New Zealand 7. B. tinantiae (Lindquist) Vánky on Tinantia fugax, from Argentina, 8. B. vuyckii (Oudem. & Beij.) Vánky on several Luzula species, from Europe, Asia, Australia and N. America, and 9. The type of the genus:

Bauerago abstrusa (G. Malençon) K. Vánky,

Mycotaxon 70:44, 1999.

Ustilago abstrusa Malençon, Bull. Soc. Mycol. France 45:256, 1929. — Cintractia abstrusa (Malençon) Ciferri, Ann. Mycol. 29:56, 1931. — Type on Juncus gerardii, France, Manche Dépt., Gatteville near Cherbourg, 19.IX.1926, leg. G. Malençon, MPU.

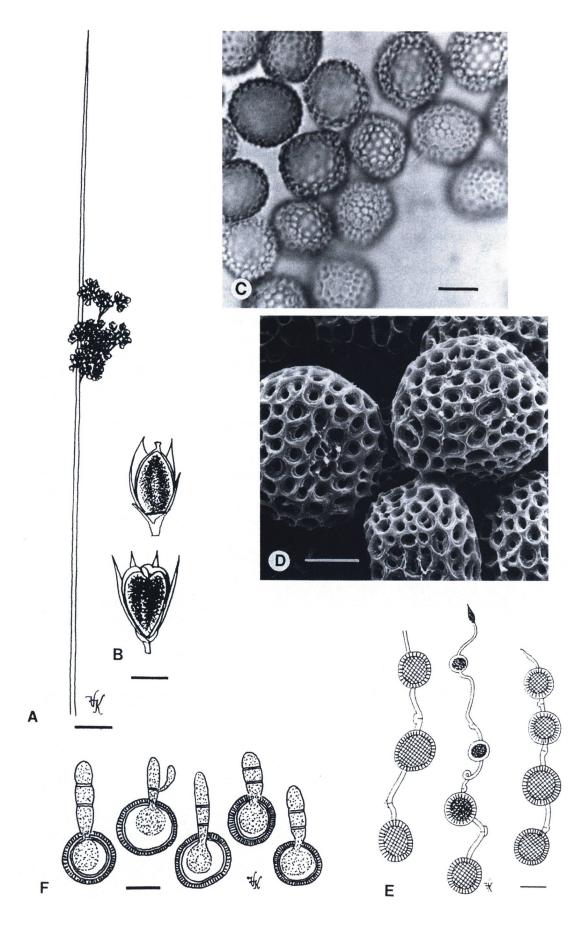
Sori (Figs. 9 A, B) in ovaries filling the capsules with golden- to cinnamon brown, dusty spore mass. Infection systemic, not causing conspicuous deformation. Spores (Figs. 9 C, D) globose, ovoid, often slightly subpolyhedrally irregular, $13-17(-18) \times 14-20(-22)$ µm, from subhyaline to lemon- or orange-yellow, finely reticulate, 7-12 meshes per spore diameter; wall 2-3 µm thick including the reticulum, muri 1-1.5 µm high, in optical median view blunt. Spores produced successively on the surface of young ovaries in the cells of sporogenous hyphae. Between cells of sporogenous hyphae clamp connections are present (Fig. 9 E). Spore germination (Fig. 9 F) results in phragmobasidia on which sessile basidiospores are produced.

On Juncaceae: Juncus balticus Willd., J. balticus × filiformis L., J. gerardii Loisel., J. gregiflorus L.A.S. Johnson; Europe, New Zealand.

Ref.: Vánky 1999b.

Fig. 9 A-E. Bauerago abstrusa on Juncus gregiflorus, Vánky, Ust. exs. no. 1002, HUV 18574.

- **A.** Sori in the seeds within the capsules. Habit (Bar = 1 cm).
- **B.** L.S. of two capsules filled with spore mass (Bar = 1 mm).
- C. D. Spores in LM and in SEM (Bar of LM picture = 10 μ m, that of SEM picture = 5 μ m).
- **E.** Spore formation in chains within each cell of the sporogenous hyphae, with clamp connections between the adjacent cells (Bar = $10 \mu m$).
- **F.** Germinating spores (on WA, at room temp., in 2 weeks; Bar = $10 \mu m$).



10. BURRILLIA W.A. Setchell,

Proc. Amer. Acad. Arts 26:18, 1891.

STEREOSORUS K. Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa, 85:45, 1943 (nom. invalid., no Latin description). — Type: S. monochoriae K. Sawada on Monochoria vaginalis (Burm. fil.) Presl ex Kunth, China, Taiwan (= Burrillia ajrekari).

Sori forming spots on paludal or aquatic plants (in Alismataceae and Pontederiaceae) containing scattered or gregarious spore balls embedded in the host tissue appearing as minute, brown dots. Spore balls composed of a parenchymatous tissue of sterile fungal cells in which numerous, pale spores are scattered irregularly or situated more or less toward the periphery of the ball; cortical layer absent. Spore germination of Tilletia-type. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore simple, with two membrane caps. Type of the genus: B. pustulata.

This is a genus of four known species in the Doassansiaceae, on aquatic or paludal plants belonging to the Alismataceae and Pontederiaceae. The genera *Burrillia, Doassansia, Entylomaster, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudodoassansia, Pseudotracya* and *Tracya*, characterized by complex spore balls, form a natural group both morphologically and ecologically and are phylogenetically related, whereas *Doassansiopsis* has the same morphology and ecology but different phylogeny (Doassansiopsidaceae), and *Doassinga* has the same ecology and phylogeny (Doassansiaceae) but different morphology (spores single, not in complex balls). The known pecies of *Burrillia are:* 1. *B. ajrekari* Thirum., 2. *B. echinodori* G.P. Clinton, 3. *B. narasimhanii* Thirum. & Mundkur, and 4. The *type of the genus:*

Burrillia pustulata W.A. Setchell,

Proc. Amer. Acad. Arts 26:18, 1891.

Doassansiopsis pustulata (Setch.) Dietel, in Engler & Prantl, Die Natürl. Pflanzenfam. I:22, 1897. — Type on Sagittaria variabilis (= S. sagittifolia), USA, Illinois, Dixon, 31.VII.1889, leg. G.P. Clinton, comm. T.J. Burrill, S; isotype HUV 9054. Topotype: on 6.VIII.1891, leg. G.P. Clinton; isotopotypes in Seymour & Earle, Econ. fgi., Suppl. C. no. 1, HUV 9601!

Sori (Fig. 10 A) on leaves, forming small, hypophyllous, irregularly orbicular, often confluent, pale yellow, slightly elevated, pustular spots. Spore balls (Fig. 10 B) embedded in the spongy parenchyma, later bursting through the epidermis, visible as minute, brown dots, subglobose to elongate-ovoid, $150-200 \times 150-350 \, \mu m$, composed of a parenchymatous tissue of sterile cells in which the spores are scattered concentrated towards the periphery of the balls; cortical layer absent. Spores (Fig. 10 B) globose, subglobose to slightly irregular, $8-10(-11) \, \mu m$ in diameter, subhyaline to pale yellow, rather firmly adhering, with smooth, c. $0.5 \, \mu m$ thick wall. Spore germination (Fig. 10 C) results in aseptate, cylindrical, c. $15 \, \mu m$ long basidia, bearing apically 4-5, slightly bent, hyaline basidiospores of c. $3 \times 16 \, \mu m$ (Setchell 1891:18).

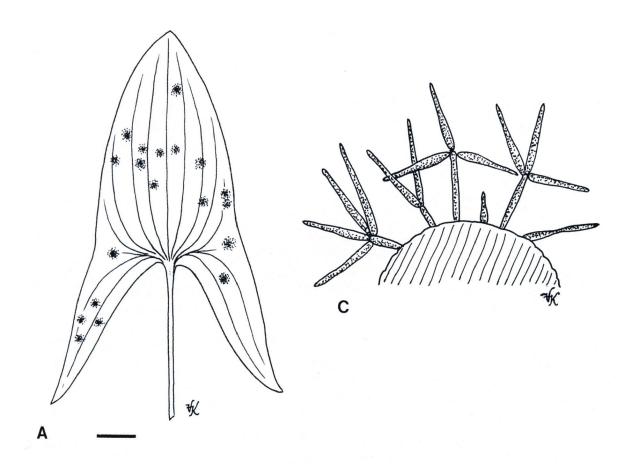
On Alismataceae: Sagittaria sagittifolia L. (S. latifolia Willd., S. variabilis Engelm.); E Asia (China), N America (Can., USA).

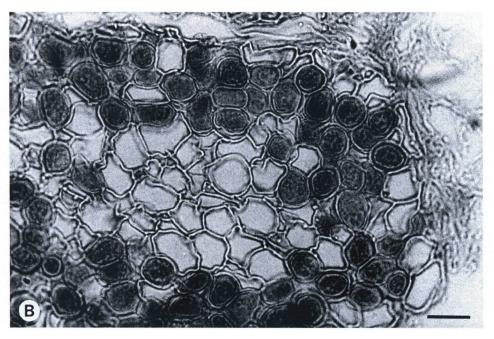
When Setchell (1891:18) described *Burrillia pustulata* he mentioned two collections without indicating the type: "Illinois, leg. G.P. Clinton, comm. T.J. Burrill" and "Wisconsin, W. Trelease". However, one year later, Setchell (1892:36) under "*Burrillia pustulata* sp. et gen. nov." indicated only the first collection as "collected the last of July, 1889".

Ref.: Setchell 1891, 1892, Thirumalachar 1947, Vánky 1981b.

Fig. 10 A-C. Burrillia pustulata on Sagittaria sagittifolia, Canada, Ontario, Pushlinch Township near Guelph, VII.1913, J. Dearness, in Sydow, Ust. no. 500, HUV 402.

A. Sori on a leaf. Habit (Bar = 1 cm). **B.** T.S. of a part of a spore ball in LM (stained; Bar = $10 \mu m$). **C.** Spore germination (in situ).





11. CENTROLEPIDOSPORIUM R.G. Shivas & K. Vánky,

Mycol. Balcan. 4:2, 2007.

Sori in the fruits of plants in Centrolepidaceae, replacing the seeds with a black, granular-powdery mass of spore balls; peridium, columella and sterile cells between the spore balls lacking. Spore balls pigmented (brown), permanent, composed of a central mass of spores surrounded by a cortex of sterile fungal cells. Spore germination results in branched hyphae on which basidiospores are formed on sterigmata. Type of the genus: C. sclerodermum.

Centrolepidosporium is currently a unispecific genus in the Ustilaginales.

Centrolepidosporium sclerodermum R.G. Shivas & K. Vánky,

Mycol. Balcan. 4:2, 2007.

Type on *Centrolepis exserta*, Australia, Northern Territory, 100 km SW of Jabiru, 10.VI.2006, leg. M.J. Ryley, M.D.E. & R.G. Shivas, BRIP 48117; isotype HUV 21360!

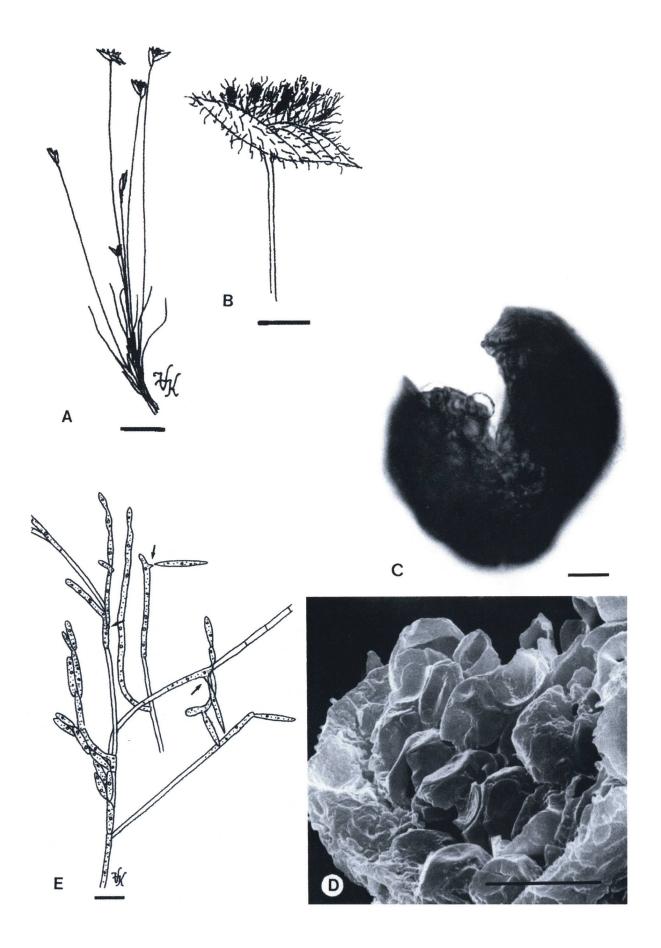
Sori (Figs. 11 A, B) in all fruits (follicles) of an inflorescence, hidden by the two bracts of the condensed inflorescence, destroying the seeds and filling the follicles with spore balls. At maturity, the follicles split longitudinally, disclosing the black, at first agglutinated, later granular-powdery mass of spore balls. Infection systemic; all follicles of an inflorescence and all inflorescences of a plant infected. Spore balls (Figs. 11 C, D) globose, subglobose, ovoid, ellipsoidal or slightly irregular, with 1-2 somewhat flattened sides, 35-60 × 40-70(-80) μm, dark reddish brown, opaque, composed of many (several tens to one hundred?), tightly packed spores surrounded by a cortex of sterile cells, that ruptures by hard pressure disclosing the spores (for spore ball and spore formation see Shivas & Vánky 2007:2). Spores (Figs. 11 C, D) rounded, subpolyhedrally or polyhedrally irregular from compaction, 5.5-7 × 6-9 μm, pale yellowish or olivaceous brown; wall thin, c. 0.5 μm, smooth. Cortex 3-4 μm thick, dark reddish brown, composed of firmly agglutinated, tangentially flattened, polyhedrally irregular sterile fungal cells, 2-10 μm in diameter, free surface irregularly crenate, in side view the profile is irregularly rough. Spore germination (Fig. 11 E) results in branched hyphae from which basidiospores are formed. Basidiospores cylindrical, ellipsoidal to fusiform, 1-1.5(-2) × 4-18 μm, producing secondary and tertiary spores in chains, on terminal and lateral sterigmata.

On Centrolepidaceae: Centrolepis exserta (R.Br.) Roem. & Schult.; Australia. Known only from the type locality.

Ref.: Shivas & Vánky 2007.

Fig. 11 A-E. Centrolepidosporium sclerodermum on Centrolepis exserta, isotype, HUV 21360.

- **A, B.** Sori in the seeds within the follicles. **A.** Habit (Bar = 1 cm). **B.** enlarged diseased inflorescence (Bar = 2 mm).
- C, D. Broken spore balls with spores surrounded by a thick cortex of sterile cells.
- **E.** Spore germination (on WA, at room temp., in 2 days) resulting in hyphae with basidiospores on short sterigmata (arrows; $Bar = 10 \mu m$).



12. CINTRACTIA M. Cornu, s. str.,

Ann. Sci. Nat. Bot., Sér. 6, 15:279, 1883.

Sori surrounding the floral axis, less often the ovaries of plants in Cyperaceae, subglobose to cylindrical, at first covered by a white or brown fungal peridium that flakes away to expose the blackish brown or black, semi-agglutinated spore mass. Spores single, dark-colored, medium-sized, formed on a mycelial stroma. Spore germination results in phragmobasidia, basidial cells often conjugating. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Type of the genus: C. axicola.

Cintractia s. str., in the Anthracoideaceae, has 11 recognized species. For a long time it was merged with *Anthracoidea*, from which it was separated by Kukkonen (1963). Recently, based partly on molecular data, it was split into several smaller genera by Piepenbring, Begerow & Oberwinkler (1999).

Cintractia axicola (M.J. Berkeley) M.M. Cornu,

Ann. Sci. Nat. Bot., Sér. 6, 15:279, 1883.

Ustilago axicola Berkeley, Ann. Mag. Nat. Hist., Ser. 2, 9:200, 1852. — Type on "some scirpoid plant" (= Fimbristylis dichotoma (L.) Vahl, det. K. Vánky), Dominican Republic, Santo Domingo, leg. M.A. Sallé 74, Herb. Berkeley no. 4745, K.

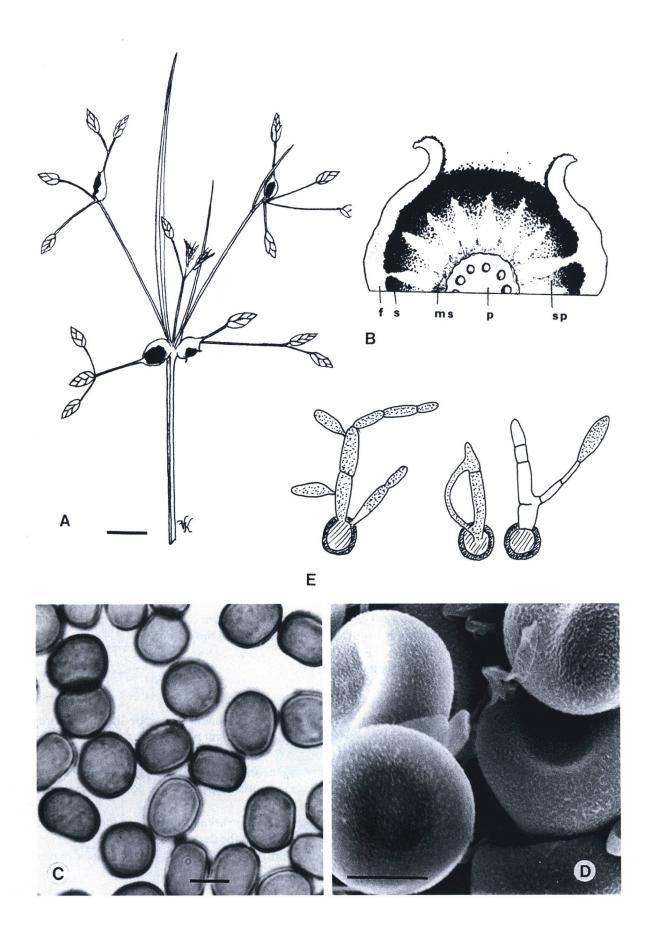
For taxonomic synonyms of *Cintractia axicola*, such as *Ustilago fimbristylis* Thümen, *C. peribebuyensis* (Speg.) Speg., *C. fimbristylidis-kagiensis* Sawada ex S. Ito, *C. suedae* Sawada ex S. Ito, *C. mundkurii* Chowdhury, *C. pilulifera* Y. Ling & T.L. Chen, *C. peribebuyensis* (Speg.) Speg. var. *major* Pavgi & Mundkur, and their literature, see Ling, *Mycologia* 42:646-647, 1950b, and Vánky 2011('2012'):94.

Sori (Figs. 12 A, B) surrounding the base of the floral pedicels, occasionally the flowers, subglobose to ovoid, 1-2 x 1-5 mm, at first covered by a white, grayish, later brown, sterile, fungal peridium which flakes away to expose the black, agglutinated spore mass developed in pockets of a hyaline, fungal stroma. Spores (Figs. 12 C, D) single, globose, ovoid to subpolyangular, usually compressed laterally, 8-15 x 12-18 μm, reddish brown; wall c. 1 μm thick, thinner and lighter colored at the flattened sides, in LM smooth to indistinctly pitted, or faintly ornamented with short, fine, sinuous striae, in SEM very finely and densely verruculose, warts partly confluent forming short, irregular, sometimes ramified striae. Spore germination (Fig. 12 E) results in 4-celled basidia. From basidial cells uninucleate, haploid basidiospores are budded off, which fuse in pairs initiating the dikaryophase. Two of the basidial cells may also fuse giving rise to dikaryotic hypha. The infection is local. The dikaryotic hyphae penetrate the epidermal cells of the host, spread inter- and intracellularly and invade the epidermis, cortex, medulla, phloem and the lignified cells of the infected peduncle. A white fungal sheath, formed of mononucleate cells, forms around the peduncle 7-10 days after infection. Under this sheath, the binucleate mycelium differentiates into stromatal tissue and sporogenous pockets. Cells of dikaryotic hyphae in the inner part of sporogenous pockets divide, giving rise to rows of spore initials which mature successively (Tommerup & Langdon, 1969).

On Cyperaceae: Fimbristylis species in the tropics and subtropics; world-wide.

Ref.: Cornu 1883, Trelease 1885, Magnus 1893b, Hirschhorn 1939b, Viégas 1940, Ling 1950a, 1950b, 1951a, Tommerup & Langdon 1965, 1969, Thirumalachar & Whitehead 1975, Nene & Bhelwa 1976, Kukkonen & Gjærum 1977, Ingold 1995a, 1999, Piepenbring, Begerow & Oberwinkler 1999, Piepenbring 2000, Vánky 2000b.

- Fig. 12 A-E. *Cintractia axicola* on *Fimbristylis dichotoma* (L.) Vahl. A, C, D. Madagascar, Prov. Tamatave, N of Fenerive, Manankinany River, 26.X.1983, L. Jonsson, HUV 11313.
- A. Sori around the floral pedicels.
- **B.** T.S. of a sorus (somewhat schematized; after Magnus 1893b). f = fungal peridium, s = spores, ms = mycelial stroma, <math>p = pedicel, sp = sporogenous pocket.
- C, D. Spores in LM and in SEM.
- E. Spore germination (after Thirumalachar & Whitehead 1975, Nene & Bhelwa 1976:41).



13. CINTRACTIELLA K.B. Boedijn,

Bull. Jard. Bot. Buitenzorg, Ser. 3, 14:368, 1937; emend. Piepenbring, Perspect. Pl. Ecol., Evol. Syst. 4:120, 2001a.

Sori in adventitious spikelets on vegetative or generative organs of the host plants in Cyperaceae (subfam. Mapanioideae), occurring in groups, forming witches' brooms. Spore mass black, initially agglutinated, enclosed in the distal part of sterile spikelets, at maturity exposed at the opened tip of the spikelet. Spores develop embedded in a hyaline, sporogenous fungal matrix, when mature solitary (not forming spore balls), relatively large and thick-walled, pigmented (reddish brown, without tint of orange-red), ornamented. Host-parasite interaction by intracellular haustoria.

Cintractiella, in the Cintractiellaceae of the order Ustilaginales, has two known species: 1. C. diplasiae (Henn.) M. Piepenbr. on Diplasia karataefolia in S America, and 2. The type of the genus:

Cintractiella lamii K.B. Boedijn,

Bull. Jard. Bot. Buitenzorg, Ser. 3, 14:370, 1937.

Type on *Hypolytrum* sp., New Guinea [= Indonesia, Irian Jaya], Prauwenbivak, IX.1920, leg. Lam 1026.

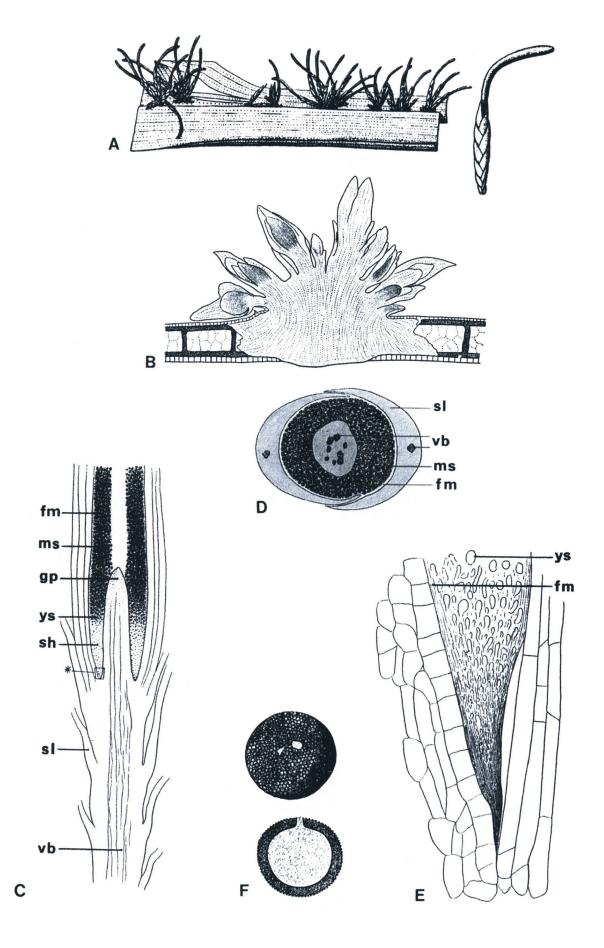
Sori (Figs. 13 A, B, C, D, E) usually hypophyllous, appearing first as hemispherical, pustular galls composed of compact parenchymatous host cells and parasitic hyphae, bursting through the epidermis. From these galls bundles of straight or curved, 1-1.5 mm wide, 5-20 mm long, somewhat flattened branches arise, invested by pale green, scale-like leaves. From the branches black, hard, cylindrical bodies grow out measuring 0.5-0.75 x 8-12 mm, composed of agglutinated spore masses surrounded by a thin (8-12 μm), subhyaline or pale yellowish membrane composed of firmly interwoven, indistinct, 1-2.5 µm thick hyphae with gelatinous walls. The parasitic hyphae from the basal pustules invade the branches and in the axils of the last pair of scale-like leaves emerge from the host tissue and form a compact ring around the growing point (Fig. 13 C). The spores differentiate within this mass of sporogenous hyphae. Only the hyphae on the periphery are unaltered, from which the covering layer around the spore mass develops. The spores are at first small, colorless, thin-walled, irregular, often elongate and wholly filled with protoplasm. Gradually they increase in size, becoming globose, and the thickened wall develops a brown color. Through the continuous spore formation and the fact that the spores strongly adhere to each other a column is formed, which projects far above the branch (Fig. 13 A), and which is also firmly held together by the covering fungal membrane. Spores (Fig. 13 F) when mature single, globose, 29-36 μm in diameter, dark brown, provided with a single germ pore; wall 3-4 μm thick, minutely reticulate. Spore germination not known. Parasitic hyphae strictly intercellular, forming coiled, lobed or often branched haustoria into the host cells.

On Cyperaceae: *Hypolytrum* sp.; Indonesia. This peculiar fungus is known only from the type collection. The type specimen of *Cintractiella lamii* is lost. Description taken from the original.

Ref.: Boedijn 1937, Piepenbring 2001a, Vánky 2003a.

Fig. 13 A-E. Cintractiella lamii on Hypolytrum sp., type (after Boedijn 1937).

- **A.** Part of a leaf with sori. Habit and enlarged a single, mature soral branch with scale-like leaves around its basal part, and the black, hard, cylindrical, curved mass of spores on its distal part.
- **B.** T.S. of a young sorus with "branch" initials.
- C. L.S. of a part of a mature branch: (vb) vascular bundles (originating from the veins of the host plant leaf), (sl) scale-like leaf, basal part, (sh) sporogenous hyphae, (ys) young spores, (gp) growing point of the branch, (ms) mature spores, (fm) fungal membrane.
- **D.** T.S. of a soral "branch" with mature spores: (sl) scale-like leaf, (vb) vascular bundles in the leaves and in the growing point, (ms) mature spores, (fm) fungal membrane surrounding the dark spore masses.
- **E.** Enlarged the last leaf branch corner (marked with an * on fig. C), filled with sporogenous hyphae: (ys) young spore, (fm) fungal membrane initial.
- F. Two spores, one in optical section.



14. *CLINTAMRA* D.I. Cordas & R. Durán, *Mycologia* 68:1244, 1977('1976').

CLINTAMRA Cordas, Ph. D. Thesis, Wash. State Univ.:11, 1971, nom. invalid. (no Latin diagnosis; ICBN/Vienna, Art. 36.1).

Sori external on the surface of young leaves and inflorescence of Dracaenaceae (Liliaceae s. lat.), forming blackish brown, granular-powdery spore mass. Spores single, in pairs or in small groups, pigmented (brown). Spore germination results in a bifurcate basidium bearing two, apical, multiseptate basidiospores. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Clintamra, in the Clintamraceae of the order Ustilaginales, is a unispecific genus. Type of the genus:

Clintamra nolinae (G.P. Clinton) D.I. Cordas & R. Durán, Mycologia 68:1244, 1977('1976').

Tolyposporella? nolinae G.P. Clinton, Proc. Boston Soc. Nat. Hist. 31:426, 1904. — Melanotaenium nolinae (G.P. Clinton) Thirumalachar, Whitehead & O'Brien, Mycologia 59:391, 1967. — Clintamra nolinae (G.P. Clinton) Cordas, Ph. D. Thesis, Wash. State Univ.:11, 1971 (comb. invalid.). — Type on Nolina microcarpa, USA, Arizona, Rincon Mt., 20.VII.1884, leg. C.G. Pringle; isotype HUV 2441!

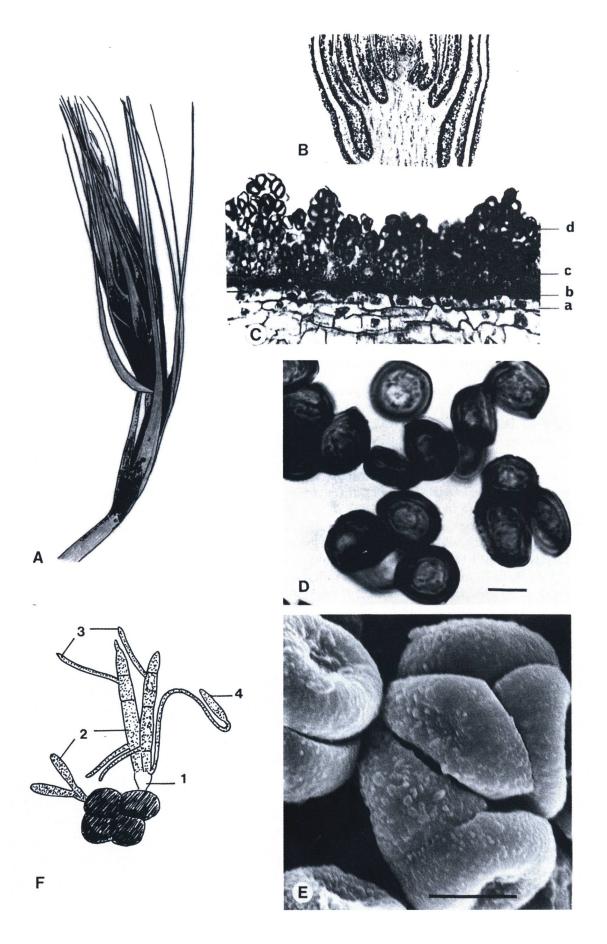
Sori (Figs. 14 A, B, C) on leaves and aborted inflorescence, usually so crowded that they form a continuous and very conspicuous layer of agglutinated, blackish brown, granular-powdery spore mass over the greater part of their surface. Spores (Figs. 14 C, D, E) single, in pairs or in rather indefinite spore balls, varying in shape and size, globose, ovoid, irregular, flattened along contiguous surfaces, 10-16 x 11-19(-22) μm, dark yellowish- to reddish brown; wall thick, 2.5-3 μm, in LM and in SEM from almost smooth to obscurely and irregularly verruculose. Spore germination (Fig. 14 F) results in a short, generally bifurcate basidium, usually bearing two, apical, oblong, multicellular basidiospores, each cell giving rise to mycelia (Durán & Safeeulla 1968, Cordas 1971).

On Dracaenaceae (Liliaceae s. lat.): *Nolina microcarpa* S. Watson, *N. texana* S. Watson; N America (Mexico, USA).

Ref.: Durán & Safeeulla 1968, Cordas 1971, Cordas & Durán 1977('1976').

Fig. 14 A-F. Clintamra nolinae on Nolina microcarpa. A-E. isotype, HUV 2441.

- **A.** External sori on aborted inflorescence. Habit.
- **B, C.** L.S. through a sorus with spores and spore balls on the surface of host tissue. a = epidermis, b = sporogenous hyphae, c = immature spores, d = mature spores. (A, B, C after Cordas & Durán 1977('1976')).
- **D, E.** Spores in LM and in SEM (Bars = $10 \mu m$).
- **F.** Spore germination. 1 = basidium, 2 = basidiospore, 3 = mycelium 4 = secondary sporidium (redrawn from Durán & Safeeulla 1968:238).



15 CONIDIOSPOROMYCES K. Vánky,

in Vánky & Bauer, Mycotaxon 43:427, 1992.

Sori in ovaries of Poaceae, scattered in the inflorescence, swollen, composed of an apically open, sac-like peridium of host tissue and fungal origin, and a central mass of a semi-powdery mixture of spores, sterile cells and balls of conidia. Columella absent. Spores relatively thick-walled, pigmented, medium-large, germinating by aseptate basidia bearing an apical cluster of elongate basidiospores. Sterile cells pale, almost colorless, ornamented or smooth, often collapsed. Conidia thin-walled, mostly Y-shaped, hyaline, arranged in more or less loose balls. Germination of basidiospores and conidia results in hyphae on which both blastic conidia and ballistospores are formed. Host-parasite interaction by intercellular hyphae, interaction apparatus is lacking. Septal pore is a dolipore traversed by two membranous plates, pore caps lacking.

The concomitant presence of conidia between the spores of *Conidiosporomyces* is a unique feature within the smut fungi. This is certainly an adaptation to an efficient dispersal under tropical conditions, where flowers susceptible to infection are continuously present during the wet season. The quickly germinating conidia repeatedly generate new infections and successive generations of the fungus. The thick-walled, resistant spores survive the dry season and start new infection cycles at the beginning of the wet season (comp. also *Heterotolyposporium*).

Conidiosporomyces, in the Tilletiaceae, has three known species: 1. C. echinospermus (Ainsw.) Vánky, 2. C. verruculosus (Wakef.) Vánky, both on Setaria spp. in Africa, and 3. The type of the genus:

Conidiosporomyces ayresii (M.J. Berkeley) K. Vánky,

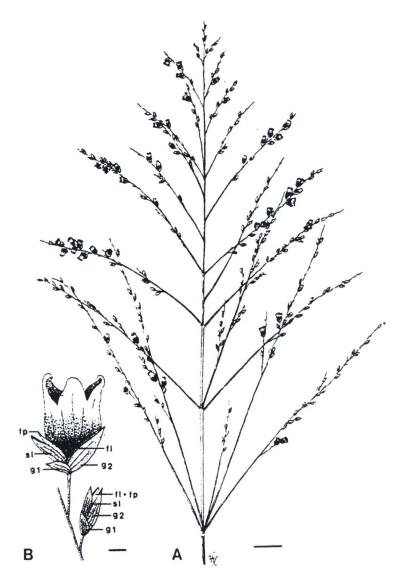
in Vánky & Bauer, Mycotaxon 43:429, 1992.

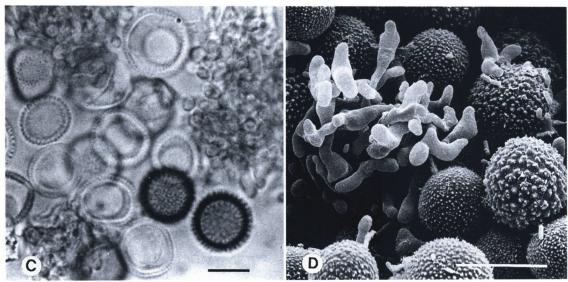
Tilletia ayresii Berk., in Massee, Bull. Misc. Inform. 1899:146, 1899. — Type on Panicum maximum (= Megathyrsus maximus), Mauritius, hills above Port Louis, leg. P.B. Ayres 4754, Herb. Berkeley in K.

Ustilago heterospora Hennings, in Engler (ed.), Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete. Teil C.:48, Berlin, 1895 (later homonym, not Niessl 1872). — Tilletia heterospora (Henn.) Zundel, Bothalia 3:310, 1938. — Type on Panicum maximum (= Megathyrsus maximus), Tanganyika Territory (Tanzania), Sk., Amboni, leg. C.H.E.W. Holst 2765. (Syn. in Zundel 1953:282).

Ustilago evansii Hennings, Bot. Jahrb. Syst. 41:270, 1908. — Type on Setaria aurea (= S. sphacelata var. aurea), South Africa, Transvaal, Tzaneen, Zoutpansberg, 9.IV.1906, leg. J.B. Davy, comm. I.B. Pole-Evans, PREM 10.; isotypes in BPI 160415, 160421. (Syn. by Vánky 2001c:313).

Sori (Figs. 15 A, B, E, F) in some ovaries of an inflorescence, inflated, ovoid or cylindrical, 1.5-3 x 2.5-5(-10) mm, composed of an apically open, sac-like, leathery peridium, and a gray to pale olivaceous brown, semipowdery central mass of spores, sterile cells and balls of conidia. Columella absent. Peridium thick, dark olivaceous or reddish brown at the base, thin, light grayish brown at its open, distal part, composed of an external layer of host tissue and an internal layer of sporogenous fungal tissue (Fig. 15 F b), restricted to the proximal half of the sorus. Peridium thickest (10-20 µm) at the base of the sorus, gradually thinning distally (Fig. 15 E). Sporogenous tissue composed of closely packed, septate, branched hyphae of c. 1.5 μm diameter. Intercellular fungal hyphae present in the proximal half of the peridium. Haustoria and clamp connections absent. Spores (Figs. 15 C, D) globose, subglobose to broadly ellipsoidal, 12-16 x 13-17 µm, yellowish brown to dark brown, finely to coarsely verrucose, warts c. 1-2 µm high, subacute or flattened, in SEM rounded, often with a short, narrow tip. Two or more warts may fuse. The size of the warts may vary not only from spore to spore but also on the same spore. Spore germination (Fig. 15 H) results in aerial holobasidia, c. 5 µm wide and up to 40 µm long, but basidia may remain included in the spore. Distal part of the basidium divided into 2-8 short branches. On short, apical tubercles of the branches 10-24 basidiospores are produced. Basidiospores (Fig. 15 H) long cylindrical, slightly curved, 2 x 30-36 μm, hyaline, germinating at both ends without conjugation, giving rise to ramified, septate hyphae on which both blastic conidia and ballistospores are produced.





Ballistospores may germinate by blastic conidia, by hyphae, by ballistospores or by Y-shaped conidia (comp. Ingold 1987a:76-78, figs. 1-3, Vánky & Bauer 1992:432-433, figs. 11-12). Sterile cells (Figs. 15 C, D) globose, subglobose, ellipsoidal, subhyaline to pale yellow, 13.5-20 x 14.5-21.5 µm, finely, moderately to densely verruculose, relatively thin-walled (1.5-2 μm), often with a large vacuole, collapsed in dried specimens. Differences between spores and sterile cells not always sharp; the relatively small, globose, thin-walled, apparently smooth, hyaline cells between the spores may be either immature spores or young sterile cells. Balls of conidia (Figs. 15 C, D) globoid, 25-55 μm in diameter, composed of many, loosely connected conidia. Spores, sterile cells and balls of conidia produced by the sporogenous hyphae on the inner side of the peridium (Fig. 15 F b) and pushed toward the center of the sorus. Conidial balls presumably produced by repetition, as in culture. Conidia (Figs. 15 C, D, I) thin-walled (c. 0.5 µm), smooth, hyaline, varying greatly in shape, usually Y-shaped, but also triangular, T-, club-, boomerang-shaped, or somewhat branched, with two rounded and widened branches and one gradually narrowing to pointed branch, 10-16(-20) µm long, usually 2.5-3 µm wide. Germination of conidia results in hyphae on which both blastic conidia and ballistospores are formed, like those produced from the germination of basidiospores. Ballistospores on MYP produce rod-shaped and Y-shaped blastic conidia, and also abundant ballistospores, Rod-shaped conidia may produce Y-shaped conidia or hyphae bearing ballistospores, Y-shaped and rod-shaped conidia. Balls of conidia formed in culture of basidiospores by repetition of Y-shaped conidia. In cultures of basidiospores on MYP, after 3 weeks, inflated, globose or ellipsoidal, hyaline, thin-walled cells were seen (possibly spores and/or sterile cell initials). Ballistospores, Yand rod-shaped conidia mononucleate in culture. Hyphal cells long, probably mononucleate. Host-parasite interaction by intercellular hyphae, interaction apparatus is lacking. Septal pore (Fig. 15 G) is of Tilletia-type, a dolipore traversed by two membranous plates, pore caps are lacking.

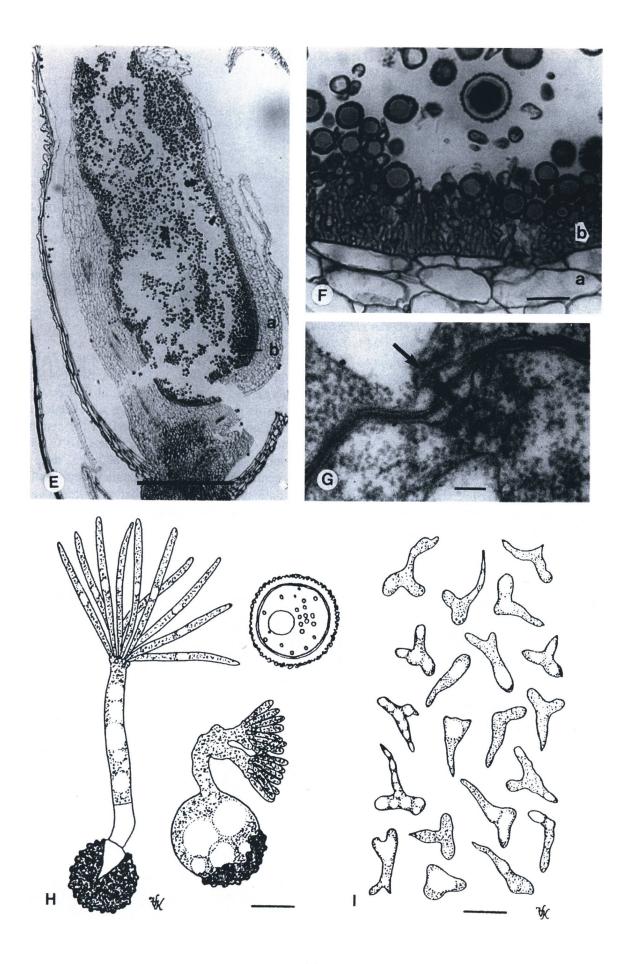
On Poaceae: Megathyrsus maximus (Jacq.) B.K. Simon & S.W.L. Jacobs (Panicum maximum Jacq.), M. maximus var. pubiglumis (K. Schum.) B.K. Simon & S.W.L. Jacobs, (Panicum maximum var. pubiglume K. Schum; P. maximum var. trichoglume Eyles ex Robyns), Panicum antidotale Retz., P. coloratum L., P. megastachyum Nees, P. parvifolium Lam., P. schinzii Hack. (P. laevifolium Hack.), Setaria pumila (Poir.) Roem. & Schult. (S. pallidefusca (Schumach.) Stapf & C.E. Hubb.; S. glauca auctt., non (L.) P. Beauv.), S. paniculifera (Steud.) Fourn. (P. paniculiferum Steud.), S. sphacelata (Schumach.) Stapf & C.E. Hubb. var. aurea (Hochst. ex A. Braun) Clayton (S. aurea Hochst. ex A. Braun); Tropical and subtropical Africa, Asia, Australia, C & S America, especially on its principal host, Megathyrsus maximus.

Probably also on additional *Megathyrsus*, *Panicum* and *Setaria* species. However, several collections and host plants given for *C. ayresii* may refer to *C. echinospermus* or *C. verruculosus*.

Ref.: Ingold 1987a, Vánky & Bauer 1992, Vánky 2001c.

Fig. 15 A-I. Conidiosporomyces ayresii on Panicum maximum, Vánky, Ust. exs. no. 814, HUV 15706.

- A. Sori in some ovaries of an inflorescence (Bar = 2 cm).
- **B.** Enlarged a sorus and a healthy spikelet. g1 = first glume; g2 = second glume; s1 = sterile lemma, with a thin, hidden palea; s1 = first lemma, and s2 = first glume; s2 = second glume; s1 = sterile lemma, with a thin, hidden palea; s1 = first lemma, and s2 = first palea, both indurate in the healthy flower, not indurate in the infected one. (Bar = 1 mm).
- C, D. Spores, sterile cells and balls of conidia in LM and in SEM.
- **E, F.** L.S. and T.S. of a sorus. a = external layer of host tissue; b = internal layer of sporogenous fungal tissue, restricted to the proximal part of the sorus, by which spores, sterile cells and balls of conidia are produced (Bars = 0.5 mm and 1 μ m, respectively).
- G. Septal pore (arrow) is a dolipore traversed by two membranous plates, pore caps are lacking (Bar = $0.1 \mu m$).
- **H.** Two germinating spores giving rise to holobasidia bearing apical, long cylindrical, slightly curved basidiospores and a hyaline, sterile cell (called also "immature spore") with trace of ornamentation.
- I. Y-, T-, club-, boomerang-shaped, triangular and irregular conidia from a sorus.



16 DERMATOSORUS K. Sawada ex L. Ling,

Mycologia 41:267, 1949.

ZUNDELULA Thirumalachar & Narasimhan, Sydowia 6:409, 1952. — Type: Z. fimbristylidis Thirum. & Naras. (= Dermatosorus fimbristylidis (Thirum. & Naras.) Langdon) on Fimbristylis sp., India. (Syn. by Langdon, 1977:450).

Sori in ovaries of Cyperaceae, swollen, covered by a peridium that ruptures irregularly, revealing the dark mass of spore balls and a more or less distinct central columella. Spore balls composed of a cortex of empty, sterile cells and a central mass of numerous fertile spores separated by small, empty compartments formed by the reticulate spore wall ornamentation of neighboring spores. Spores pigmented (brown), medium-sized. Spore germination results in phragmobasidia with sessile basidiospores. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Dermatosorus, in the Anthracoideaceae, is a uniform genus, with six known species in the tropics and subtropics (studied by Vánky 1987b). *Type of the genus:*

Dermatosorus eleocharidis K. Sawada ex L. Ling,

Mycologia 41:268, 1949.

Doassansia eleocharidis (Sawada ex L. Ling) Ciferri, Quad. Lab. Crittog. Ist. Bot. Univ. Pavia 27:18, 1963.

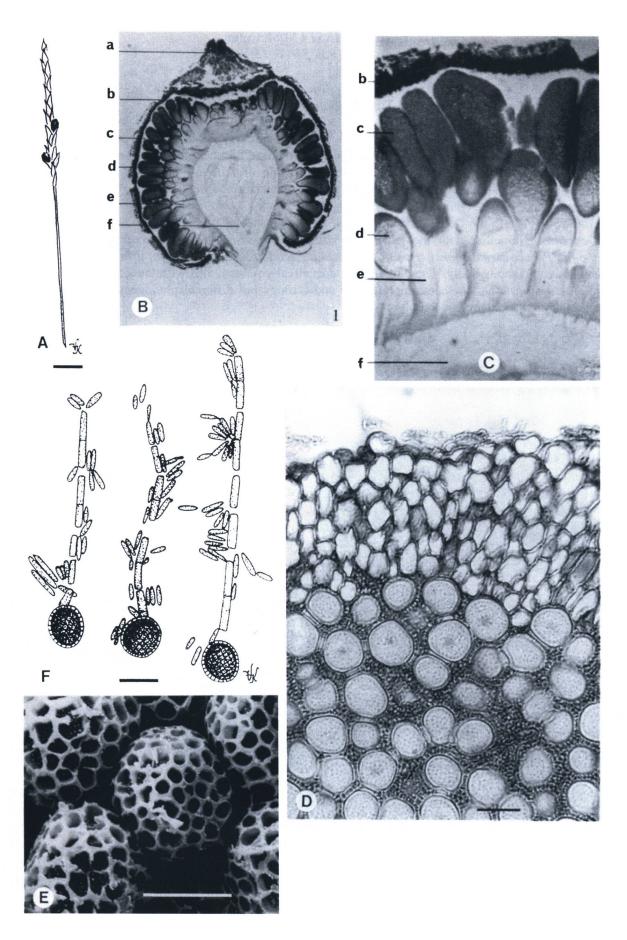
— Type on Eleocharis dulcis, Taiwan, Kang-shan, Kao-hsiung, 10.IV.1919, leg. Y. Shimada, BPI 194103.

Sori (Figs. 16 A, B) in scattered ovaries, swollen, subglobose, 2-2.5 mm in diameter, at first covered by a firm, thick, black peridium composed of the ovary wall and a delicate layer of hyphae, which later ruptures irregularly, revealing an aggregate of dark, large spore balls. Columella well developed, in the center of the sorus, composed of an indurate mass of hyphae and remnants of ovule. *Spore balls* (Figs. 16 C, D) rather permanent, irregularly polyhedral, ovoid, elongate, rarely subglobose, 90-350 x 110-600 μm, deep brown, opaque, composed of a cortex of sterile, fungal cells, and a central mass of spores separated by small, empty compartments of c. 0.5-1 μm diameter, formed by the reticulate spore wall ornamentation of the neighboring spores. Spore balls differentiate successively from the hyphal initials amassed over the columella, ripening from their distal part (Fig. 16 C). Loosely packed non-sporogenous hyphae surround the spore balls, extending from the columella just inside the ovary wall. Sporulation ceases with senescence of the spike of the host. *Spores* globose to ovoid, 6.5-12 μm in diameter, reddish brown, loosely united by their ornamentation; wall reticulate, c. 1.5-2 μm thick, in SEM interspaces finely verruculose. *Cortex* of the spore balls rather permanent, 15-75 μm thick, consisting of 4-6 layers of firmly united, dark reddish brown sterile cells, 3-6.5 μm in diameter; wall 0.5-1 μm thick, apparently smooth. Infection local, in inflorescence. *Spore germination* results in phragmobasidia with sessile basidiospores.

On Cyperaceae: *Eleocharis dulcis* (Burm. fil.) Trin. ex Hensch., *E. philippinensis* Svenson, *E. sphacelata* R.Br.; E & SE Asia (China, Thailand), Australia.

Ref.: Ling 1949, Thirumalachar & Narasimhan 1952, Pavgi & Giri 1966, Singh & Pavgi 1970, 1977a, Langdon 1977, Vánky 1987b, 1995a, Piepenbring, Bauer & Oberwinkler 1998.

- **Fig. 16 A-D.** *Dermatosorus eleocharidis* on *Eleocharis philippinensis* Svenson. Australia, Queensland, near Ipswich, 20.II.1975, R.F.N. Langdon, HUV 7179.
- **A.** Sori in some ovaries of the host plant. **B.** L.S. of a young sorus and **C.** a part of it, enlarged. a = remnants of the style, b = sorus membrane, c = mature spore balls, d = immature spore balls, e = non-sporogenous hyphae, f = columella (Langdon 1977:448). **D.** Part of a spore ball (T.S.) showing the multilayered cortex of empty sterile cells and the central mass of rounded spores separated by minute compartments formed of the outermost, reticulate layer of the spores.
 - E-F. Dermatosorus cyperi Vánky on Cyperus aff. celluloso-reticulatus Böckler, type, HUV 15991.
- **E.** Single spores in SEM with the reticulum which in the balls, with the reticulum of the neighboring spores, form the empty "cells" (Bar = 5 μ m). **F.** Spore germination (on WA, at 30 °C, in 1 day) results in 6-8-celled basidia on which sessile, evoid to ellipsoidal basidiospores are produced.



17 DOASSANSIA M.M. Cornu,

Ann. Sci. Nat. Bot. Sér. 6, 15:285, 1883.

SETCHELLIA Magnus, Verh. Bot. Vereins Prov. Brandenburg 37:91, 1896('1895'). — Type: S. punctiformis (Niessl) Magnus (= Doassansia niesslii de Toni) on Butomus umbellatus L., Germany.

Sori in leaves, petioles and stems of paludal or aquatic plants, in both mono- and dicotyledonous families, forming pale green, yellowish or brownish areas with numerous spore balls embedded in the host tissue appearing as minute, brown dots. Spore balls persistent, composed of a central mass of spores surrounded by a more or less distinct cortex of sterile cells. Spore germination of Tilletia-type. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore simple, with two membrane caps. Type of the genus: D. alismatis.

Doassansia belongs to the Doassansiaceae. It has 12 known species on both mono- and dicotyledonous host plants. Doassansia, together with the genera Burrillia, Entylomaster, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudodoassansia, Pseudotracya and Tracya, forms a natural group both morphologically and ecologically. They all are phylogenetically related, also with the single-spored Doassinga, whereas Doassansiopsis has the same morphology and ecology but different phylogeny, reflected in different ultrastructural and molecular characters.

Doassansia alismatis (C.G. Nees) M.M. Cornu,

Ann. Sci. Nat. Bot. Sér. 6, 15:285, 1883.

Sclerotium alismatis Nees, in E. Fries, Syst. Myc., etc., Vol. 2, sect. 1:257, 1822. — Perisporium alismatis (Nees) E. Fries, Syst. Myc., etc. Vol. 3, sect. 1:252, 1829. — Doassansia alismatis (Nees) C. Fisch, Ber. Deutsch. Bot. Ges. 2:415, 1884 (comb. superfl.). — Doassansia alismatis (Nees) J. Schröter, in Cohn, Krypt. Fl. Schles. 3(1):286, 1887 (comb. superfl.). — Type on Alisma "natans" (= misnamed A. plantago-aquatica L., det. Liro 1938:485), Germany, leg. C.G. Nees von Esenbeck, HAL.

Dothidea alismatis Lasch, in Rabenhorst, Herb. viv. myc. no. 553, 1844. nom. nud.; in L. Kirchner, Lotos 6:205, 1856 (as "Dothidea Alismatis Leach"). — Type on Alisma plantago-aquatica, Germany, Dresden, leg. W.G. Lasch; isotypes in Rbh., Herb. viv. myc. no. 553, HUV 9573!

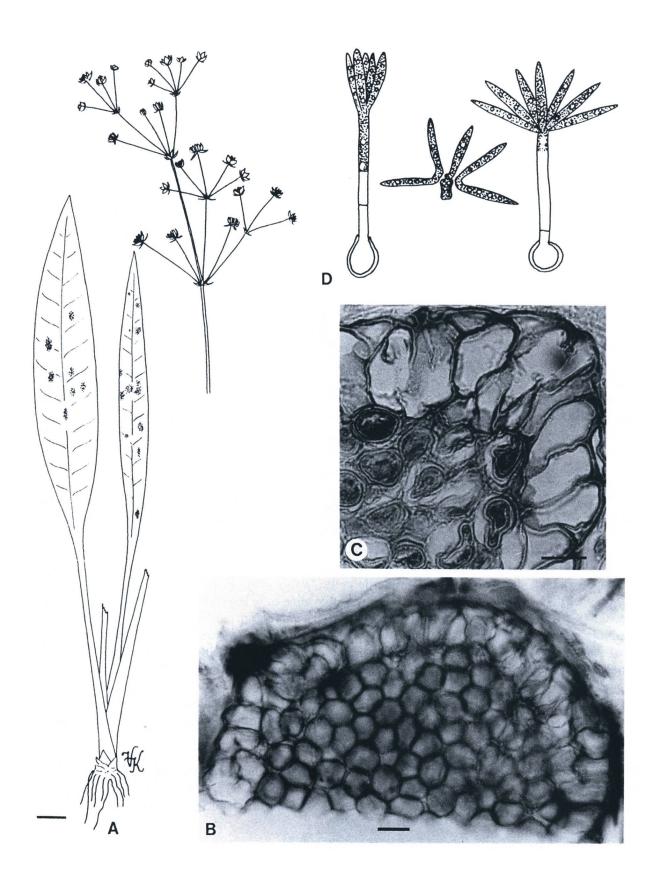
Sori (Fig. 17 A) in leaves at first as yellowish white, later pale to dark brown, orbicular or elongate spots, 1-15 mm in diameter or larger when coalesced, sometimes covering most of the leaf surface, with spore balls embedded in the host tissue appearing as numerous, raised, minute, dark brown dots. *Spore balls* (Figs. 17 B, C) globose, ovoid to slightly irregular, 110-220(-250) μm, composed of a central mass of spores surrounded by a cortex of one, occasionally partly two layers of sterile cells. *Spores* (Figs. 17 B, C) globose, subglobose, ovoid or slightly irregular, subpolyhedral, 7-11 x 9.5-15 μm, yellowish hyaline; wall thin, c. 0.8 μm, smooth. *Cortical cells* (Figs. 17 B, C) firmly united, without spaces between them, varying in shape and size, mostly radially elongate, polyhedral, irregular or occasionally subglobose or flattened, 5-13 x 8-25 μm, yellowish brown, with smooth, 1-1.5 μm thick wall. *Spore germination* (Fig. 17 D) of *Tilletia*-type (Setchell 1892:5, figs. 1-32, Brefeld, 1895:190, Pl. XI, figs. 17-19).

On Alismataceae: Alisma gramineum Lej., A. lanceolatum With., A. orientale (Sam.) Juz., A. plantago-aquatica L., A. plantago-aquatica var. parviflorum Torr., Damasonium alisma Mill. (A. damasonium L.), D. minus (R.Br.) Buchenau; Europe, Africa, Asia, Australia, N America.

Anamorph (Savulescuella alismacearum (Sacc.) Cif.) reported but probably refers to basidiospores of spores that germinated in situ (comp. Lutman 1910:1211; Zambettakis 1959). Ramularia alismatis Fautrey is often mistaken for the anamorph of Doassansia alismatis.

Ref.: Hohenbühel-Heufler 1884, Fisch 1884, de Toni 1888b, Setchell 1891, 1892, Magnus 1895, Flerov 1924, Liro 1938, Thirumalachar 1946, 1947, Zambettakis 1959, Patil & Gandhe 1975, Vánky 1981b, Azbukina & Govorova 1986a, Azbukina 1990.

Fig. 17 A-C. *Doassansia alismatis* on *Alisma lanceolatum*, Romania, Satu-Mare, 6.VI.1966, K. Vánky, HUV 436. A. Sori on the leaves. Habit (Bar = 1 cm). B. Part of a spore ball, hand-cut section, unstained (Bar = $10 \mu m$). C. Part of a spore ball, sectioned with microtome, stained. D. Spore germination (after Setchell 1892, Pl. I).



18 DOASSANSIOPSIS (W.A. Setchell) P. Dietel,

in Engler & Prantl, Die Natürl. Pflanzenfam. I(1)**:21, 1897.

DOASSANSIA Cornu subgen. DOASSANSIOPSIS Setchell, Proc. Amer. Acad. Arts 26:16, 1891.

Sori in leaves, petioles, stems or ovaries of aquatic or paludal plants, in both mono- and dicotyledonous families, as spots or swellings. Spore balls embedded in the host tissue, persistent, composed of a central mass of sterile, parenchymatous fungal cells surrounded by the firmly adhering, colorless spores, and an external cortex of sterile cells. Spore germination of Tilletia-type. Host-parasite interaction by haustoria. Septal pore simple, with membrane caps and two plates closing the pore.

The Doassansiopsidaceae family contains only one genus, *Doassansiopsis*, with 14 known species, parasitizing mono- and dicotyledonous host plants in the Alismataceae (5), Limnocharitaceae (1), Menyanthaceae (2), Nymphaeaceae (4) and Potamogetonaceae (2). Morphologically and ecologically *Doassansiopsis* is close to the members of Doassansiaceae (*Burrillia*, *Doassansia*, *Entylomaster*, *Heterodoassansia*, *Nannfeldtiomyces*, *Narasimhania*, *Pseudodermatosorus*, *Pseudodoassansia*, *Pseudotracya* and *Tracya*) but phylogenetically it is not related to them (Bauer *et al.* 1997). *Doassansiopsis* represents a beautiful example ofconvergent evolution, due to adaptation to a parasitic life cycle on aquatic or paludal plants. *Lectotype of the genus* (design. by Clements & Shear 1931:339):

Doassansiopsis deformans (W.A. Setchell) P. Dietel,

in Engler & Prantl, Die Natürl. Pflanzenfam. I(1)**:21, 1897.

Doassansia deformans Setchell, Proc. Amer. Acad. Arts 26:17, 1891. — Lectotype on Sagittaria variabilis (= S. sagittifolia), (design. by Vánky 2002a:48) Canada, London, IX.1890, leg. J. Dearness, HUV 475!; isolectotypes in Ellis & Ev., N. Amer. fgi., Ser. 2, no. 2705 (as Doassansia deformans).

Doassansia horiana Hennings, Bot. Jahrb. Syst. 37:157, 1906. — Doassansiopsis horiana (Henn.) C.I. Chen (as 'C.I. Shen'), Sinensia 4:319, 1934. — Doassansiopsis horiana (Henn.) Y. Nisikado & H. Matsumoto, Ber. Ohara Inst. Landw. Forsch. Kurashiki 7:425, 1936 (comb. superfl.). — Type on Sagittaria sagittifolia, Japan, Tokyo, Nashigahara, VIII.1904, leg. S. Hori 34, SAPA; isotypes BPI 178362, 195044, HUV 16633! (Syn. by Vánky 2007a:54).

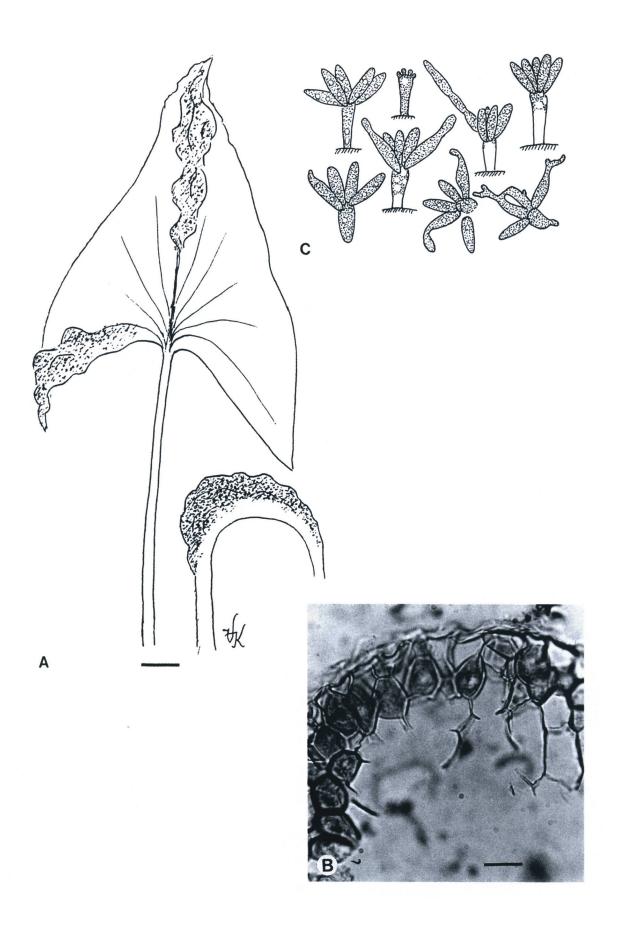
Sori (Fig. 18 A) in leaves, petioles, stems and inflorescence as brown, bullate pustules or swellings, often causing conspicuous distortions, from a few mm to 7-8 cm long, filled with spore balls embedded in the host tissue. Spore balls (Fig. 18 B) globose, subglobose, ovoid, elongate or irregular, 70-150(-220) x 90-180(-250) μm, pale yellowish brown, composed of a central mass of sterile, parenchymatous, empty cells surrounded by a layer of spores and a thin cortical layer of sterile cells. Spores (Fig. 18 B) globoid, ovoid, radially elongate, usually polyhedrally irregular, 7-11 x 9-17(-20) μm, subhyaline to pale yellowish brown, contents homogenous; wall c. 0.5 μm thick, smooth. Sterile cells (Fig. 18 B) varying in shape and size, rounded or elongate, polyhedrally irregular, 4-17 x 6-30 μm, empty, subhyaline to pale yellow tinted; wall c. 0.5 μm thick, smooth. Cortical sterile cells (Fig. 18 B) varying in shape and size, small, usually radially more or less flattened, subcuneiform, irregularly polyhedral, tangentially 5.5-15 μm long, pale yellowish brown, empty; wall c. 0.5 μm thick, smooth. Spore germination of Tilletia-type (Setchell 1892).

On Alismataceae: Sagittaria lancifolia L., S. montevidensis Cham. & Schlecht., S. sagittifolia L. (S. latifolia Willd., S. variabilis Engelm.), S. trifolia L., S. trifolia var. sinensis (Sims.) Makino; E Asia (China, Japan), N, C & S America (Canada, USA, Honduras, Brazil), W Indies (Cuba).

Ref.: Setchell 1891, 1892, 1894, Nisikado & Matsumoto 1936, Thirumalachar 1947, Vánky 1981b.

Fig. 18 A-C. Doassansiopsis deformans on Sagittaria sagittifolia. Lectotype, HUV 475.

- A. Sori on a deformed leaf and petiole.
- **B.** Part of a spore ball (hand sectioned, stained with cotton blue).
- C. Spore germination (after Setchell 1892, Pl. I).



19. *DOASSINGA* K. Vánky, R. Bauer & D. Begerow, *Mycologia 90*:965, 1998.

Sori on aquatic or paludal plants (in Callitrichaceae) producing spots. Spores solitary, poorly pigmented, embedded in the host tissue. Spore germination of Tilletia-type, resulting in holobasidia. Host-parasite interaction (Fig. 4, p. 23) by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore is simple, with two membrane caps.

Doassinga belongs to the Doassansiaceae family, occupying a basal position there, as ultrastructural and molecular biological characters showed (Vánky, Bauer & Begerow 1998). In contrast to the other ten genera of this family (e.g. Burrillia, Doassansia, Entylomaster, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudodoassansia, Pseudotracya and Tracya), Doassinga has single spores, not agglutinated in spore balls which usually are composed also of sterile cells and/or modified mycelia (comp. Pl. I., pg. 17, chapter Introduction). Doassinga is currently unispecific with its type:

Doassinga callitrichis (J.I. Liro) K. Vánky, R. Bauer & D. Begerow, *Mycologia 90*:965, 1998.

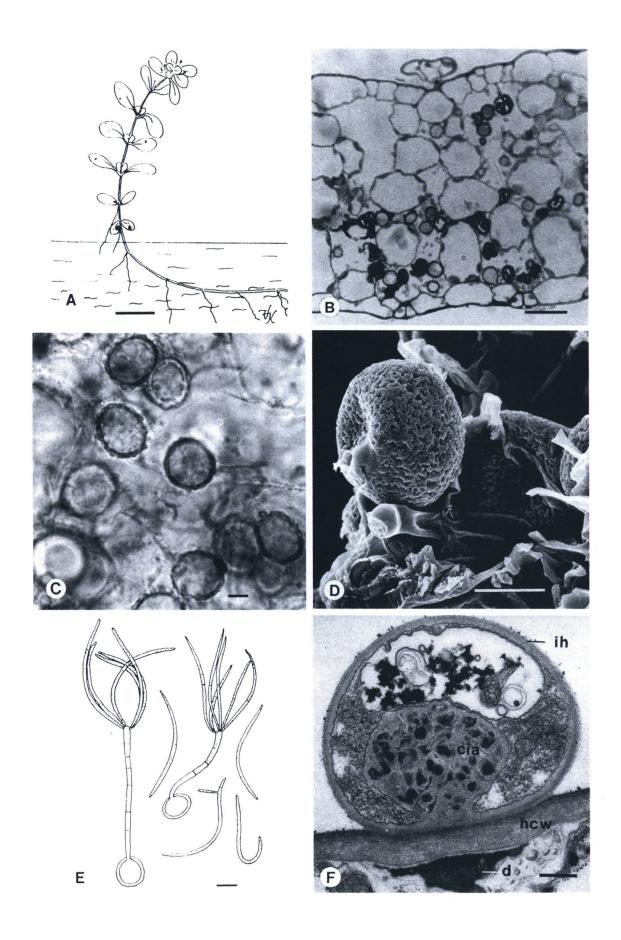
Entyloma callitrichis Liro, Ann. Acad. Sci. Fenn., Ser. A, 42(1):118, 1938 (nom. inval., no Latin diagnosis); Mycotheca fennica. Die Etiketten. No. 301-600:113, 1939. — Type on Callitriche verna (= C. palustris), Finland, Nylandia, Pornainen, 19.VIII.1917, leg. J.I. Liro, H.

Sori (Figs. 19 A, B) in the leaves and stems as indistinct, greenish yellow to pale yellowish brown spots, 0.5-1.5 mm or larger by confluence, with indefinite margins. Spores embedded in the host tissue (Figs. 18 B, C, D), scattered between the parenchyma cells of the host plant, globose, ovoid to broadly ellipsoidal, (8-)9-13.5 x 10-16 μm, hyaline to pale yellow; wall smooth, verruculose to low tuberculate, c. 1 μm thick. Spore germination (Fig. 19 E) results in aseptate basidia bearing apically 4-8, long, fusiform or sigmoid basidiospores of 1-1.5 x 15-60 μm. Parasitic hyphae intercellular, lacking haustoria. Host-parasite interaction characterized by complex interaction apparatus containing cytoplasmic portions (Fig. 19 F & Fig. 4, p. 23). Septal pore is simple, with rounded pore lip and on both sides with a membrane cap. Molecular analysis shows a close relationship with members of the Doassansiaceae. The described anamorph, Entylomella callitrichis Liro (1938:118), represents the basidiospores of in situ germinated spores.

On Callitrichaceae: Callitriche palustris L. (C. verna L.), C. stagnalis Scop.; Europe.

Ref.: Liro 1938, 1939, Vánky, Bauer & Begerow 1998.

- Fig. 19 A-F. Doassinga callitrichis on Callitriche stagnalis, Vánky, Ust. exs. no. 560 (as Entyloma callitrichis), HUV 12657.
- A. Sori as indistinct spots on the leaves.
- **B.** T.S. of a sorus with scattered spores embedded in the parenchymatic leaf tissue (Bar = $100 \mu m$).
- C, D. Spores in LM and in SEM.
- **E.** Spore germination resulting in holobasidia with retraction septa, bearing apically 4-8 fusiform or sigmoid basidiospores.
- **F.** Host-parasite interaction: intercellular hypha (ih) attached to a host cell wall (hcw) showing a complex interaction apparatus within the fungal cell (but outside the fungal cytoplasm) with portions of a highly branched, cisternal net containing electron-opaque material (cia). Opposite to the complex interaction apparatus electron-opaque deposits (d) can be seen adjacent to the host plasma membrane (Bar = $0.33~\mu m$, photo R. Bauer).



20. *EBALLISTRA* R. Bauer, D. Begerow, A. Nagler & F. Oberwinkler, *Mycol. Res.* 105:423, 2001.

Sori as black spots in leaves and stems of Poaceae. Spores solitary or in groups but not aggregated in balls, pigmented (olive-brown), embedded in the host tissue, not erumpent, not powdery. Spore germination results in holobasidia with gastroid (not ballistic) basidiospores. Parasitic hyphae mostly intercellular. Host-parasite interaction apparatus lacking. Septal pore absent.

Eballistra, in the Eballistraceae within the Georgefischeriales, has three known species. Certainly, the number of the species will increase with germination and/or molecular studies of further "Melanotaenium" and dark-spored "Entyloma" species on Poaceae and Cyperaceae (comp. also Phragmotaenium). The known Eballistra species are: 1. E. brachiariae (Viégas) R. Bauer, Begerow, A. Nagler & Oberw. on Brachiaria and Urochloa species, from Africa, Asia, Australia, S America, 2. E. lineata (Cooke) R. Bauer, Begerow, A. Nagler & Oberw. on Zizania aquatica L., from Asia and North America, and 3. The type of the genus:

Eballistra oryzae (H. & P. Sydow) R. Bauer, D. Begerow, A. Nagler & F. Oberwinkler, Mycol. Res. 105:423, 2001.

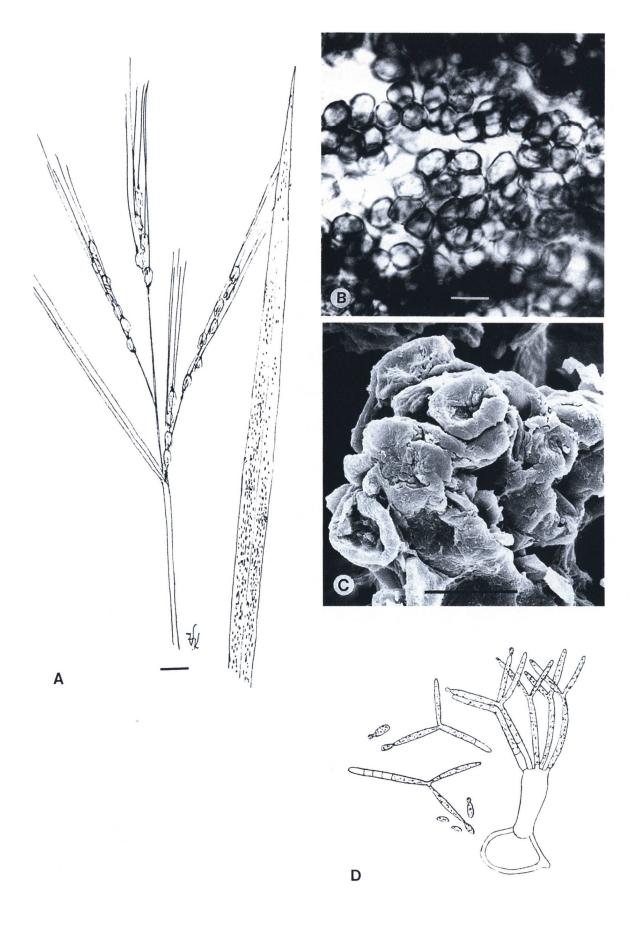
Entyloma oryzae H. & P. Sydow, Ann. Mycol. 12:197, 1914. — Type on Oryza sativa, Philippines, Laguna Prov., Los Banos, 20.XII.1913, leg. M.B. Raimundo (C.F. Barker no. 2203).

Sori (Fig. 20 A) in leaves and leaf sheaths as small, angular or short linear spots, 0.5-1 x 0.5-2 mm, lead-colored, usually not confluent. Spores (Figs. 20 B, C) embedded in the host tissue, agglutinated but not forming spore balls, varying in shape and size, rarely subglobose, ellipsoidal or elongate, usually subpolyhedrally irregular, with one or several flattened sides, 5.5-8 x 6-11 μm, olivaceous brown; wall uniformly c. 0.5 μm thick, smooth. Spore germination (Fig. 20 D) results in holobasidia on which several apically and passively released triradiate (Y-shaped) basidiospores are produced; basidiospores germinate by budding, giving rise to yeast colonies in culture.

On Poaceae: Oryza latifolia Desv., O. sativa L., cultivated rice; cosmopolitan, in the tropics and subtropics.

Ref.: Sydow H. & P. 1914, Joshi 1963, Bauer, Begerow, Nagler & Oberwinkler 2001.

- **Fig.** 20 **A-C.** *Eballistra oryzae* on *Oryza sativa*, Vánky, Ust. exs. no. 910 (as *Entyloma oryzae*), HUV 16399. **A.** Sori on a leaf.
- B, C. Spores in LM and in SEM.
- **D.** Spore and basidiospore germination. A germinating spore with a holobasidium, apically bearing several elongate, passively released, "triradiate" basidiospores. Two basidiospores germinate giving rise to budding yeast cells in culture (after Bauer *et al.* 2001).



21. ENTORRHIZA C.A. Weber,

Bot. Zeitung (Berlin) 42:378, 1884.

SCHINZIA Nägeli, Linnaea 16:281, July-August, 1842 (not Schinzia Dennstedt, 1818), sensu Magnus.

Sori as galls on roots of Juncaceae and Cyperaceae. Spores formed intracellularly, terminally on the hyphae, usually solitary, thick-walled, embedded in the host tissue. Spore germination of Entorrhiza-type with a 4-celled basidium that remains within the spores, each basidial cell developing a branch bearing apically and subapically up to four falcate, looped or curved basidiospores. Host-parasite interaction (Fig. 2, p. 22) by local interaction zones, lacking interaction apparatus; coiled, septate haustoria present. Septal pore dolipore, without membranous plates or caps. Type of the genus: E. cypericola.

Entorrhiza, with 14 known species, belongs to the Entorrhizaceae of the order Entorrhizales, subcl. Entorrhizomycetidae. Fineran (1978b) studied the genus at a time when only five species were known. The genus was merged with *Melanotaenium* by Thirumalachar & Whitehead (1968), an unfortunate solution. These two genera differ markedly in their morphological, biological and ultrastructural characters and also in their phylogeny.

Entorrhiza cypericola (P. Magnus) C.A. Weber,

Bot. Zeitung (Berlin) 42:378, 1884.

Schinzia cypericola Magnus, Verh. Bot. Vereins Prov. Brandenburg 20:54, 1878. — Entorrhiza cypericola (Magnus) de Toni, in Saccardo, Syll. Fung. 7:498, 1888 (comb. superfl.). — Melanotaenium cypericola (Magnus) Thirumalachar & Whitehead, Amer. J. Bot. 55:185, 1968. — Type on Cyperus flavescens, Germany, near Berlin, Grunewald, Halensee, VIII.1876, leg. C. Müller, HBG.

Entorrhiza cyperi Brefeld, Unters. Gesammtgeb. Mykol. 15:80, 1912, nom. nud. — On Cyperus flavescens, Germany.

Sori (Figs. 21 A, B) on roots forming at first whitish, later pale yellowish to dark brown, elongate, cylindrical, fusiform, usually branched galls, up to 15 mm long, in which the spores are produced intracellularly. Spores (Figs. 21 C, D) subellipsoidal to ellipsoidal, (11-)12.5-15.5(-19) x (12.5-)14.5-21(-28) μm, pale yellow to pale reddish brown; wall 1.5-5 μm thick, rugulose-undulate, sometimes smooth, two-layered but some spores have an additional third, thick, hyaline, smooth outer layer, in SEM the spore surface appears irregular, tuberculate to cerebriform. Spores in pairs may be present. Host-parasite interaction (Fig. 2, p. 22) by local interaction zones, lacking interaction apparatus, haustoria present. Septal pore is a dolipore without membranous plates or caps.

On Cyperaceae: Cyperus flavescens L.; Europe, N Africa.

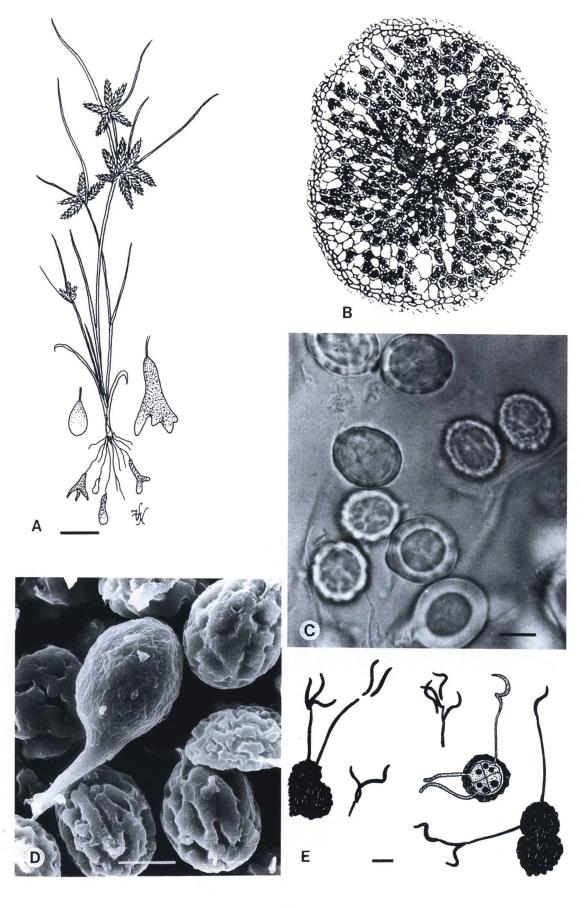
Spore germination of *Entorrhiza casparyana* (Magnus) Lagerh. on *Juncus articulatus* L. (Fig. 21 E) results in 4-celled basidia produced within the spores by formation of two, perpendicular septal walls. Each basidial cell germinates producing up to four falcate, looped or curved basidiospores on the top of a shorter or longer hyphal branch (Fineran 1982).

Ref.: Weber 1884, Lagerheim 1888, Magnus 1888, 1893a, Correns 1897, Ferdinandsen & Winge 1914, Liro 1938, Thirumalachar & Whitehead 1968, Fineran J. 1971, 1978a, 1978b, 1980, 1982, 1983, Bandoni, Maze & Delange 1979, Deml & Oberwinkler 1981, Fineran B. & J. 1984, Vánky 1992, 1998d, Bauer, Oberwinkler & Vánky 1997.

Fig. 21 A-D. Entorrhiza cypericola on Cyperus flavescens.

A. Sori on the roots forming galls. **B.** T.S. of a sorus, with the intracellularly formed spores (after Magnus 1893a). **C, D.** Spores in LM and in SEM, Vánky, Ust. exs. no. 47, HUV 590.

E. Spore germination of *Entorrhiza casparyana* (Magnus) Lagerh. from *Juncus articulatus* L. (on WA, at room temp., in a few days, stained with cotton blue. Sori were kept previously in water, at 7 °C, for several months until they were more or less decomposed; after Fineran 1982).



22. ENTYLOMA A. de Bary,

Bot. Zeitung (Berlin) 32:101, 1874.

Sori in vegetative parts of dicotyledonous host plants, mostly in leaves and stems, usually forming spots, sometimes pustules, swellings or galls. Spores solitary or adhering in irregular groups, permanently embedded in the host tissue, hyaline, yellow or pale yellowish brown; spore wall usually smooth, often with a hyaline gelatinous sheath. Spore germination of Tilletia-type. Host-parasite interaction (Fig. 3, p. 22) by simple interaction apparatus, haustoria absent. Septal pore simple, with two membrane caps. Anamorph: Entylomella Höhnel, often present.

Entyloma, in the Entylomataceae, has about 180 species on host plants belonging to 25 families, most of them on Asteraceae (86 species). It was an extremely heterogeneous genus from which numerous species and groups were excluded or separated. Several "Entyloma" species have been shown to belong to the Protomycetales, Chytridiales, Uredinales, Peronosporales, Hyphomycetes and to other groups of fungi (for these see Vánky 1994:454-456). Savile (in Savile & Parmelee 1964:708) separated from Entyloma the new genus Ustilentyloma, and Vánky (1981b) the genus Nannfeldtiomyces. The dark-spored genera Eballistra, Jamesdicksonia, Phragmotaenium (Bauer et al. 2001), as well as Melanustilospora (Denchev 2003) were also recognized or separated from Entyloma. It was demonstrated (Bauer, Oberwinkler & Vánky 1997) that the genus Melanotaenium is a good genus (in Melanotaeniaceae). Begerow et al. (2002) concluded that "phylogenetic relationships in the genus Entyloma are a result of joint evolution with their hosts". This means that the host plant criterion can be a useful tool in species delimitation in this group of smuts in which spore morphology has little variability and differences are difficult to describe. However, because the same Entyloma species can infect several host plant species, the host plant criterion in species delimitation within the genus has to be used with care. A critical study with modern methods of the genus is required. Lectotype of the genus:

Entyloma microsporum (F. Unger) J. Schröter,

in Rabenhorst, Fgi. eur. no. 1872, 1874.

Protomyces microsporus Unger, Die Exantheme der Pflanzen, etc.:343, Wien, 1833. — Entyloma ungerianum de Bary, Bot. Zeitung (Berlin) 32:101, 1874 (nom. nov. superfl. pro P. microsporus). — Type on Ranunculus repens L., Austria, Tirol, Kitzbühel, leg. F. Unger.

Caeoma bullosum Saccardo, Nuovo Giorn. Bot. Ital., N.S., 22:32, 1915. — Type on Ranunculus chaerophyllus L., Malta I., Uied il Kleigha, III.1914, leg. A. Caruana-Gatto & G. Borg. (Syn. by Sydow 1924:290).

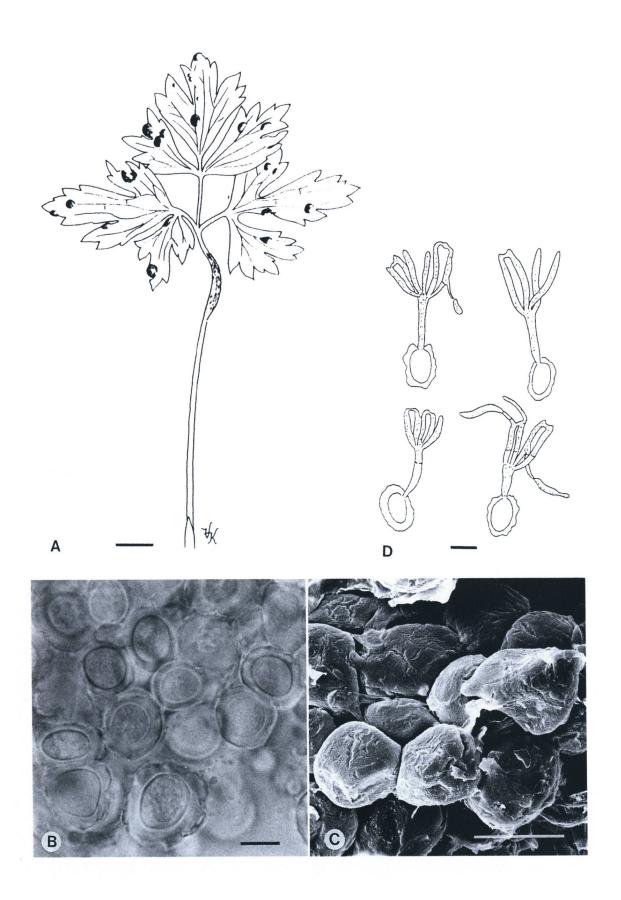
Entyloma microsporum (Unger) J. Schröter var. pygmaeum Allescher, in Allescher & Hennings, Biblioth. Bot. 12:40, 1897 (n.v.). — Entyloma pygmaeum (Allescher) Ciferri, Ann. Mycol. 26:51, 1928. — Type on Ranunculus pygmaeus Wahlenb., Greenland. (Syn. by Ciferri 1963b:151, as E. ungerianum).

Sori (Fig. 22 A) in leaves and petioles as hard pustules or swellings, at first yellowish white, disk-like, later brown, swollen, subglobose or fusiform, wart-like, with cracked surface. Spores (Figs. 22 B, C) embedded in the host tissue, crowded, globose, ovoid or irregular, 10-16 x 11-23 μm, pale yellow; wall two-layered, inner layer yellow, uniformly c. 0.5-1 μm thick, outer layer hyaline, uneven, 1-9 μm thick, smooth. Spore germination (Fig. 22 D) results in aseptate basidium developing an apical whorl of 4-8 simultaneously produced basidiospores, which fuse in pairs giving rise to septate and ramified mycelia and/or to secondary ballistospores. Anamorph absent.

On Ranunculaceae: at least on 24 Ranunculus species; cosmopolitan.

Ref.: de Bary 1874, Schröter 1877a, 1877b., Stempell 1934, Kaiser 1936, Liro 1938, Savile 1946a, 1946b, 1947, Das 1949, Brady 1953, 1960, Azbukina & Govorova 1986b, Begerow, Bauer & Boekhout 2000, Begerow, Lutz & Oberwinkler 2002, Piątek 2005b.

Fig. 22 A-C. *Entyloma microsporum* on *Ranunculus repens* L., Vánky, Ust. exs. no. 63, HUV 1157 (LM), and no. 826, HUV 15718 (SEM picture). **A.** Sori on a leaf and petiole. **B, C.** Spores in LM and in SEM (Bars = 10 μm). **D.** Spore germination (on WA, at room temp., in 2 days; after Vánky, Bauer & Begerow 1998:969).



23. ENTYLOMASTER K. Vánky & R.G. Shivas,

Mycol. Balcan. 3:15, 2006.

Sori on host plants in Araceae forming leaf spots containing spores agglutinated in irregular balls, embedded in the host tissue. Spore balls composed of spores only, without a fungal cortex, without sterile cells. Spores pale colored (yellow, pale yellowish brown or orange-yellow, without blackish or reddish brown tint), produced on the top of sporogenous hyphae. Hyphae intercellular. Septal pore simple, enclosed by two membrane caps. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions. Haustoria absent.

Entylomaster belongs to the Doassansiaceae, together with Burrillia, Doassansia, Doassinga, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudodoassansia, Pseudotracya and Tracya, characterized by spore balls (except for Doassinga), similar ultrastructure and aquatic or paludal host plants. Two species of Entylomaster are known parasitizing plants in the Araceae: 1. Entylomaster dietelianus (Bubák) Vánky & R.G. Shivas, on Ambrosina bassii L., from Italy and Morocco, and 2. The type of the genus:

Entylomaster typhonii K. Vánky & R.G. Shivas,

Mycol. Balcan. 3:15, 2006.

Type on *Typhonium brownii*, Australia, Queensland, c. 250 km NNW of Brisbane, 55 km WNW of Gympie, Mt. Sinai near Kilkivan, 13.IV.1968, leg. J.M. Simmonds 18995, BRIP 8669; isotypes IMI 153737, HUV 20221!

Sori (Figs. 23 A. B) as rounded or ellipsoidal leaf spots, c. 0.5-1 cm in diam. or larger by confluence, sometimes covering almost the entire lamina, yellowish brown, with numerous spore balls permanently embedded in the leaf tissue as minute, densely situated, dark brown dots, evident especially on the abaxial surface. Spore balls (Figs. 23 C, D, E) formed of several, small groups of aggregated spores. The small groups are globose or ellipsoidal, c. 30-60 μm in diameter, honey-yellow, composed of ten to several tens of spores that are tightly adhering or separated by remnants of fungal hyphae. Small balls grouped into irregular balls of 100-200 μm in diam., or larger by further agglomeration, pale to dark orange-yellow to brick-red, composed of hundreds of spores that separate by pressure. Fungal cortex around the balls lacking, but the large spore balls sometimes surrounded by a thin layer of compressed host cells. Spores (Figs. 23 C, D, E) globose, subglobose, ellipsoidal, rarely irregular, with one or two flattened sides, 11-14.5(-16) × 11-15(-17.5) μm, lemon-, honey- to orange-yellow; wall more or less uniformly 1-1.5 μm thick, smooth; spore profile often slightly undulate due to the remnants of surrounding empty hyphae. Spores formed intercellularly on the top of sporogenous hyphae. Sterile cells between the spores or spore balls absent. Spore germination not known.

On Araceae: Typhonium brownii Schott; Australia. Known only from the type collection.

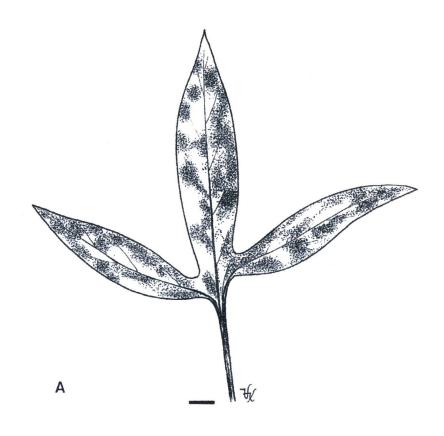
Ref.: Vánky & Shivas 2006.

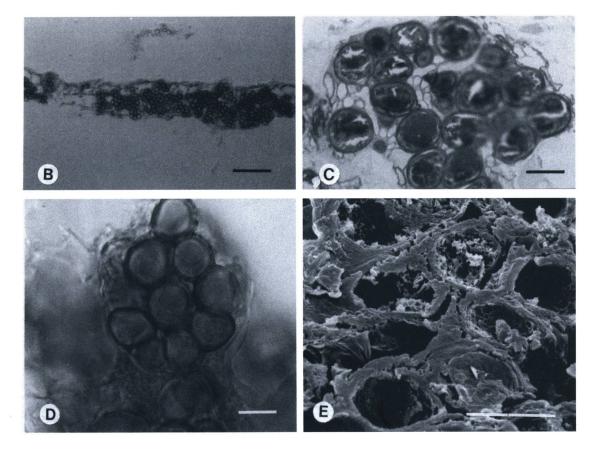
Fig. 23 A-E. Entylomaster typhonii on Typhonium brownii, isotype, HUV 20221.

A. Sori on a leaf. Habit (Bar = 1 cm).

B, C. T.S. of a leaf with spore balls embedded in the leaf tissue (stained; Bar of Fig. B = $100 \mu m$, that of Fig. C = $10 \mu m$).

D, E. Spore balls composed of spores, in LM and in SEM (sectioned; Bars = $10 \mu m$).





24. ERIOCAULAGO K. Vánky,

Mycol. Balcan. 2:113, 2005.

Sori in ovaries of host plants in Eriocaulaceae, filling the capsules with dark colored spore masses, no peridium, no columella. *Spores* single, pigmented (brown), without violet or yellowish red tint. *Sterile cells* lacking. *Spore germination* results in phragmobasidia producing basidiospores.

Eriocaulago, with an uncertain systematic position, has two known species, 1. E. jagdishwari (Mishra) Vánky, on Eriocaulon and Syngonanthus spp., India, Thailand, and 2. The type of the genus:

Eriocaulago eriocauli (G.E. Massee) K. Vánky,

Mycol. Balcan. 2:114, 2005.

Cintractia eriocauli Massee, Grevillea 22:67, 1894. — Ustilago eriocauli (Massee) G.P. Clinton, J. Mycol. 8:137, 1902. — Ustilago eriocauli (Massee) Ciferri, Ann. Mycol. 26:31, 1928 (comb. superfl.). — Type on Eriocaulon fenestratum, Madagascar Central, leg. Baron, comm. W.J. Hooker, K; isotype BPI 160374.

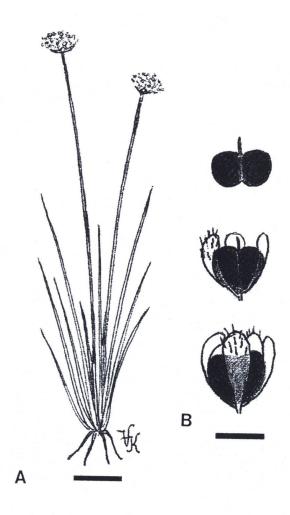
Ustilago eriocauli G.P. Clinton, Rhodora 3:82, 1901. — Type on Eriocaulon septangulare (= E. aquaticum), USA, Massachusetts, South Billerica, 17.XI.1900, leg. G.P. Clinton, BPI 160378; isotypes BPI 160375, Seymour & Earle, Econ. fgi., Suppl. C. no. 68, HUV 9660! (Syn. by Clinton 1902:137).

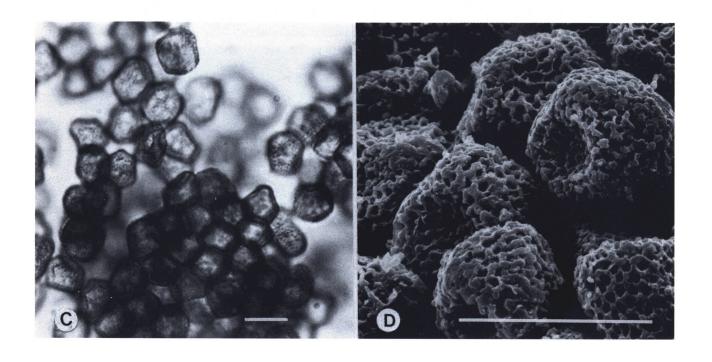
Sori (Figs. 24 A, B) in the capsules appearing as ovoid or usually laterally flattened, distinctly two lobed, blackish, rather hard bodies, c. 0.7-1 mm long and 0.8-1.2 mm wide, hidden by the perianth, filled with a dark reddish brown, agglutinated mass of spores, no sterile cells. Spores (Figs. 24 C, D) subpolyhedrally or polyhedrally irregular, more rarely rounded, ovoid or elongate, $8-10.5 \times 9.5-16 \mu m$, pale olivaceous brown; wall even, c. 0.5 μm thick, in LM appearing as densely verruculose, spore profile finely wavy to finely, densely serrulate, in SEM densely verruculose, warts confluent, forming small, incomplete or complete meshes, then appearing foveolate. Spore germination (Clinton 1901:82) results in 4-celled basidia producing terminal and lateral basidiospores measuring $1.5-3 \times 6-12 \mu m$.

On Eriocaulaceae: *Eriocaulon aquaticum* (Hill) Druce (*E. septangulare* With.; *E. articulatum* (Huds.) Morong), *E. fenestratum* Bojer ex Körn.; Africa (Madagascar), N America (USA).

Ref.: Clinton 1901, Vánky 2005c.

- Fig. 24 A-D. *Eriocaulago eriocauli* on *Eriocaulon aquaticum*, isotype of *Ustilago eriocauli* G.P. Clinton, Seymour & Earle, Econ. fgi., Suppl. C. no. 68, HUV 9660.
- A. Sori in the capsules. Habit (Bar = 1 cm).
- **B**. Three enlarged infected capsules (Bar = 1 mm).
- C, D. Spores in LM and in SEM (Bars = $10 \mu m$).





25. *ERIOCORTEX* K. Vánky & R.G. Shivas, in Vánky, Shivas, Barrett & Lutz, *Mycobiota 1*:11, 2013.

Sori in ovaries of host plants in Eriocaulaceae, filling the capsules with dark colored masses of spore balls. Fungal peridium, columella and sterile cells lacking. *Spore balls* composed of spores and a hard cortex. *Spores* pigmented (yellowish brown, without violet or red tint). *Type of the genus: Eriocortex eriocauli*.

Eriocortex is a unispecific genus with uncertain systematic position within the Ustilaginales. Type of the genus:

Eriocortex eriocauli R.G. Shivas, K. Vánky, M.D. Barrett & M. Lutz, in Vánky, Shivas, Barrett & Lutz, *Mycobiota* 1:11, 2013.

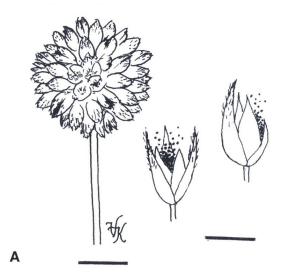
Type on *Eriocaulon scullionii* G.J. Leach, Australia, Western Australia, Kimberley Region, 3 km NNE of Prince Regent River from E boundary of Prince Regent Nature Reserve (1 km E of reserve), alt. c. 570 m, 22.IV.2008, leg. R.L.Barrett 4560B. Holotype BRIP 54346, isotype HUV 21964.

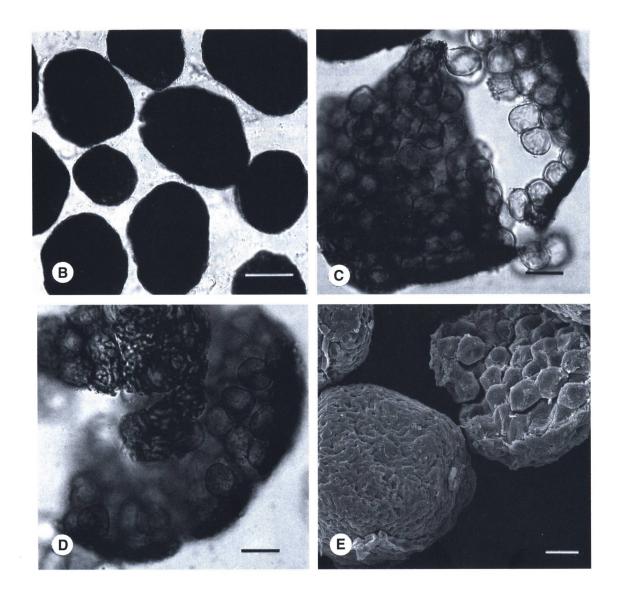
Sori (Fig. 25 A) in some capsules of an inflorescence, filling them with a black, granular-powdery mass of spore balls, replacing the ovaries, liberated by the opening of the capsules but hidden by the floral envelopes. Spore balls (Figs. 25 B, C, D) globose, ovoid, broadly ellipsoidal, subpolyhedrally, rarely triangularly irregular, 40-120 × 45-145 μm, dark reddish brown, subopaque, permanent, breaking by hard pressure, composed of several tens to some hundreds of tightly packed, easily separating spores, and a thin, dark, hard, fungal cortex. Spores (Figs. 25 C, D) globose, ellipsoidal to rounded subpolyhedrally irregular, 8-12 × 8.5-14 μm, pale yellowish brown; wall even, thin, c. 0.5 μm thick, smooth. Cortex (Fig. 25 B. C) 2-4 μm thick, dark reddish brown, composed of tightly packed, interwoven and conglutinated structure of short or elongated, irregular, often bent or even ramifying sterile fungal cells, 1.5-2.5 μm wide, 8-20 μm long; wall slightly uneven, 0.5-1 μm thick. Sterile cells absent.

Ref.: Vánky, Shivas, Barrett & Lutz 2013.

Fig. 25 A-D. Eriocortex eriocauli on Eriocaulon scullionii G.J. Leach, isotype, HUV 21964.

- A. Sori in some capsules of an inflorescence. Habit (Bar = 3 mm) and two enlarged flowers with capsules filled with spore balls (Bar = 1 mm).
- **B.** Spore balls in LM (Bar = $40 \mu m$).
- C, D. Ruptured spore balls showing the spores and the dark cortex enclosing the spores in LM (Bars = $10 \mu m$).
- E. A broken spore ball with spores and part of an intact spore ball covered by the cortex in SEM (Bar = $10 \mu m$).





26. ERIOMOESZIA K. Vánky,

Mycol. Balcan. 2:106, 2005.

Sori in ovaries of host plants in Eriocaulaceae, filled by permanent spore balls, columella lacking. Spore balls composed of a mass of tightly agglutinated spores separated by sterile cells, surrounded by a cortical layer of sterile cells. Spores pigmented (brown), without violet or yellowish red tint. Sterile cells between the spores thinwalled, pigmented (brown), empty. Spore germination results in phragmobasidia producing basidiospores. Infection systemic. Host-parasite interaction by intracellular hyphae. Mature septa poreless.

Eriomoeszia is a unispecific genus with uncertain systematic position within the Ustilaginales. It seems closely related with *Moesziomyces* on Poaceae. *Type of the genus*:

Eriomoeszia eriocauli (G.P. Clinton) K. Vánky,

Mycol. Balcan. 2:106, 2005.

Tolyposporium eriocauli G.P. Clinton, Rhodora 3:82, 1901. — Dermatosorus eriocauli (G.P. Clinton) M.D. Whitehead & Thirumalachar, Mycologia 64:128, 1972. — Tolypoderma eriocauli (G.P. Clinton) Thirum., in Thirumalachar & Neergaard, Friesia 11:191, 1978('1977') (nom. inval., Tolypoderma being a nom. nud., ICBN/Vienna, Art. 43.1). — Moesziomyces eriocauli (G.P. Clinton) Vánky, Nord. J. Bot. 6:71, 1986. — Type on Eriocaulon septangulare (= E. aquaticum), USA, Massachusetts, at Ellis, 10.IX.1900, leg. G.P. Clinton, BPI 192598; isotypes in Seymour & Earle, Econ. fgi., Suppl. C. no. 54, HUV 7953!

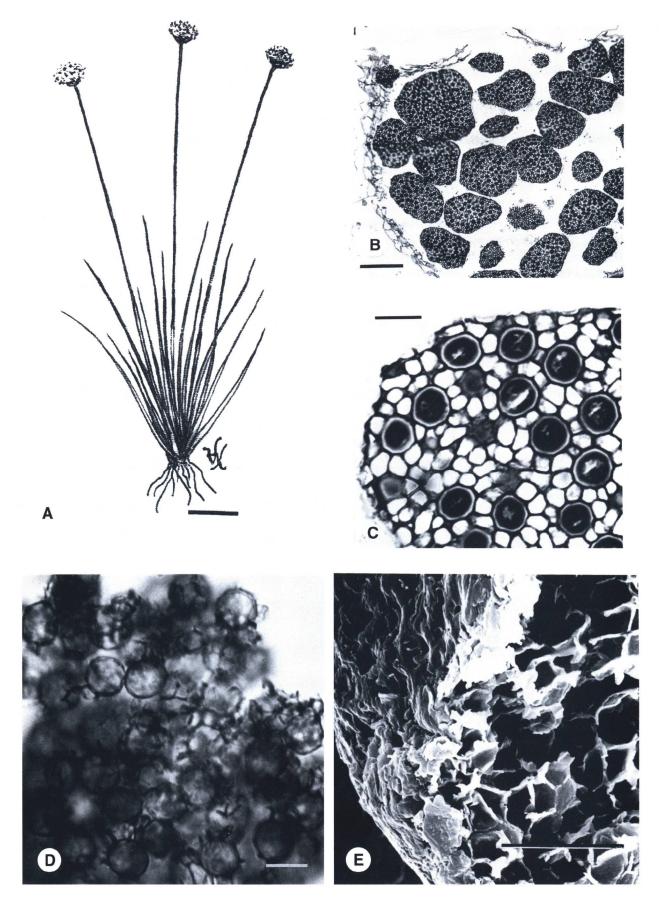
Sori (Figs. 26 A, B) in all flowers of an inflorescence as obovoid, slightly flattened, often two lobed, or rounded three lobed bodies, the swollen capsules, up to 2 mm long, hidden by the perianth, covered by a thin membrane of host origin that ruptures easily disclosing the blackish brown, granular-powdery mass of spore balls. Infection systemic. Both female and male flowers of an inflorescence affected, developing capsules and replacing the ovaries with spore balls (transvestitism). Usually all inflorescences of an infected plant affected. Spore balls (Figs. 26 B, C, E) ovoid or irregular, rarely globose, 65-160 × 70-200(-250) μm, dark brown, opaque, composed of a mass of hundreds of spores separated by sterile cells which at the same time also hold the spores together in the ball. A thin, hard, cortical layer of sterile cells covers the balls. Spores (Figs. 26 C, D, E) globose to ovoid or almost subpolyhedral, $7-9 \times 8-11 \mu m$, pale yellowish brown; wall thin (in LM c. 0.5 μm , in TEM 1-2 µm), finely, densely, low verrucose as seen in SEM. Sterile cells (Figs. 26 C, E) between the spores varying in shape and size, irregularly polyhedral, up to 7 µm long, yellowish brown, empty at maturity; wall thin, 0.15-0.4 µm (measured in TEM), smooth. In squash preparation the sterile cells rupture irregularly and their fragments remain firmly attached to the spores as winged reticulations, spines or wrinkles. Cortex (Figs. 26 C, D, E) formed of small, firmly united, relatively thick-walled, sterile cells arranged in a single, continuous layer, empty, in face view rounded, ovoid, elliptical or subpolygonally slightly irregular, 4-6.5 × 4-7.5 μm, dark yellowish brown, in side view 3-5 µm high, with four more or less flattened sides; lateral walls fused with those of the neighboring cells, 0.5-0.8 µm thick, free wall in LM slightly convex or concave, much thinner, especially in its center, when dry impressed, in SEM surface finely verruculose. At a 40x magnification, the spore balls appear shiny due to the presence of the small-celled cortical layer. Spore germination (Clinton 1901:80) results in septate basidia bearing laterally and terminally basidiospores.

On Eriocaulaceae: *Eriocaulon aquaticum* (Hill) Druce (*E. septangulare* With.; *E. articulatum* (Huds.) Morong), *E. cinereum* R.Br., *E. collinum* Hook. fil.; S Asia (India), N America (USA).

Ref.: Clinton 1901, Vánky 2005b.

Fig. 26 A-E. Eriomoeszia eriocauli on Eriocaulon aquaticum, isotype, HUV 7953.

A. Sori in the inflorescence, hidden by the floral envelopes. Habit (Bar = 1 cm). **B.** T.S. of a sorus with spore balls (stained; Bar = $100 \mu m$). **C.** Part of a spore ball (sectioned, stained; Bar = $10 \mu m$). **D.** A squashed spore ball in LM, with separated spores because of the ruptured sterile cells (Bar = $10 \mu m$). **E.** Part of a ruptured spore ball in SEM, with spores, ruptured sterile cells and the cortex (Bar = $10 \mu m$).



27. ERIOSPORIUM K. Vánky,

Mycol. Balcan. 2:114, 2005.

Sori in ovaries of host plants in Eriocaulaceae, filling the capsules with spore balls. Fungal peridium, columella and sterile cells lacking. *Spore balls* composed of spores only, sterile cells and cortical layer lacking. *Spores* pigmented (brown), without violet or yellowish red tint.

Eriosporium, with an uncertain taxonomic position within the Ustilaginales, has currently two species: **1.** *E. hessii* (E. Müller) Vánky, on *Eriocaulon lanatus* H. Hess from Angola, and **2.** The *type of the genus*:

Eriosporium mesanthemi (E. Müller) K. Vánky,

Mycol. Balcan. 2:114, 2005.

Sorosporium mesanthemi E. Müller, Phytopathol. Z. 23:109, 1955. — Lectotype on Mesanthemum radicans, Angola, Bié Prov. (design. by Vánky 2005c:114), Baixo Cubango, 176 km NW of Cuangar, alt. 1070 m, 29.I.1952, leg. H. Hess 52/514, Z+ZT. Syntype on M. radicans, Angola, Bié Prov., 61 km S of Caiundo, alt. 1160 m, 4.II.1952, leg. H. Hess 52/614, Z+ZT (both types extremely scanty).

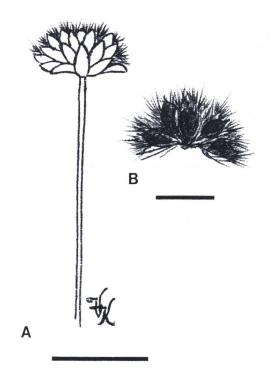
Sori (Figs. 27 A, B) in the ovaries filling the capsules with spore balls, appearing as broadly ellipsoidal, obovoid or lemon shaped bodies, c. 0.5-1 × 0.8-1.2 mm, often with an acute tip, the remnant of the style, hidden by the perianth, initially covered by a thin, grayish membrane of host origin (the remnants of the capsule), that ruptures irregularly disclosing the black, semi-agglutinated to granular-powdery mass of spore balls. Columella and fungal peridium lacking. *Spore balls* (Figs. 27 C, D) varying greatly in shape and size, mostly subpolyhedrally or even polyhedrally irregular, often elongate, more rarely globose, triangular or curved, 30-80 × 40-100(-120) μm, medium dark yellowish brown, apparently loose but rather permanent, composed of tens to hundred(s)? of spores which separate by pressure. No cortex around the balls, no sterile cells between the spores. *Spores* (Figs. 27 C, D) subglobose, ovoid, ellipsoidal to rounded subpolyhedrally slightly irregular, 5.5-8(-9)x 6.5-9.5(-10) μm, pale yellowish brown; wall even, c. 0.5 μm thick, apparently smooth, in SEM with low, inconspicuous warts. *Spore germination* unknown.

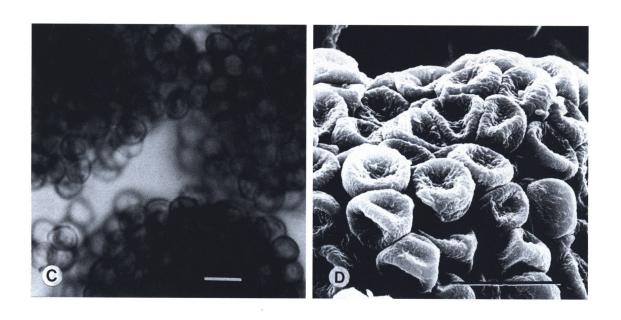
On Eriocaulaceae: Mesanthemum radicans Körn.; Africa (Angola).

Ref.: Müller 1955, Vánky 2005c.

Fig. 27 A-D. Eriosporium mesanthemi on Mesanthemum radicans. Lectotype, Z+ZT.

- A. Sori in all capsules of an inflorescence, hidden by the floral envelopes. Habit (Bar = 1 cm).
- **B.** Some enlarged, infected capsules, with some perianths removed (Bar = 4 mm).
- C, D. Spore balls and spores in LM and in SEM (Bars = $10 \mu m$).





28. ERRATOMYCES M. Piepenbring & R. Bauer,

Mycologia 89:930, 1997.

Sori forming dark, not bursting spots or pustules on leaves of Fabaceae. Spores single, pigmented (brown), embedded in the host tissue, scattered in the intercellular spaces. Spore germination of Tilletia-type with holobasidia apically carrying needle-shaped basidiospores. Host-parasite interaction by intercellular hyphae, interaction apparatus is lacking. Septal pore a dolipore traversed by two membranous plates, pore caps lacking. Growth in culture producing hyphae and ballistospores.

Erratomyces, in the Erratomycetaceae, order Tilletiales, is related to *Tilletia* from which it differs by host plants in a dicotyledonous family, by spores embedded in the leaf tissue, and by molecular phylogenetic characters (Castlebury et al. 2005, Figs. 3 & 4). *Tilletia sterilis* Ule has spores also embedded in the leaf tissue but on plants in Poaceae (*Koeleria, Poa* and *Festuca*), and has other DNA characters. Five species of *Erratomyces* are known, all on Fabaceae: 1. *E. ajmeriensis* (J.C.S. Gupta) M. Piepenbr. & R. Bauer on *Sesbania* spp., 2. *E. crotalariae* (N.C. Joshi) M. Piepenbr. & R. Bauer on *Crotalaria*, 3. *E. smithiae* (Thirum., V.V. Bhatt, Patel & G.W. Dhande) M. Piepenbr. & R. Bauer on *Smithia*, 4. *E. thirumalacharii* (Pavgi) M. Piepenbr. & R. Bauer on *Sesbania* spp., and 5. The *type of the genus*:

Erratomyces patelii (M.S. Pavgi & M.J. Thirumalachar) M. Piepenbring & R. Bauer, Mycologia 89:933, 1997.

Protomycopsis patelii Pavgi & Thirumalachar, Nature 172:315, 1953 (nom. nov. pro Synchytrium phaseoli Patel, Y.S. Kulkarni & G.W. Dhande, Curr. Sci. 18:171, 1949, a later homonym, not S. phaseoli Weston, in Chardón & Toro 1930). — Protomycopsis phaseoli (Patel, Y.S. Kulk. & G.W. Dhande) K. Ramakr. & Subram., in Subramanian & Ramakrishnan, J. Madras Univ., Sect. B, 26:367, 1956 (n.v.; comb. illeg.). — Type on Phaseolus mungo (= Vigna mungo), India, Bombay Presidency [= Maharashtra State], East Khandesh, Jalgaon, government farm, VIII.1948.

Entyloma vignae Batista, Bezerra, Ponte & Vasconcelos, Atas Inst. Micol. 3:147, 1966. — Type on Vigna sinensis, Brazil, Ceará State, Fortaleza, 7.VIII.1965, leg. J.J. da Ponte 50694 "IMUFP". (Syn. by Piepenbring & Bauer 1997:934).

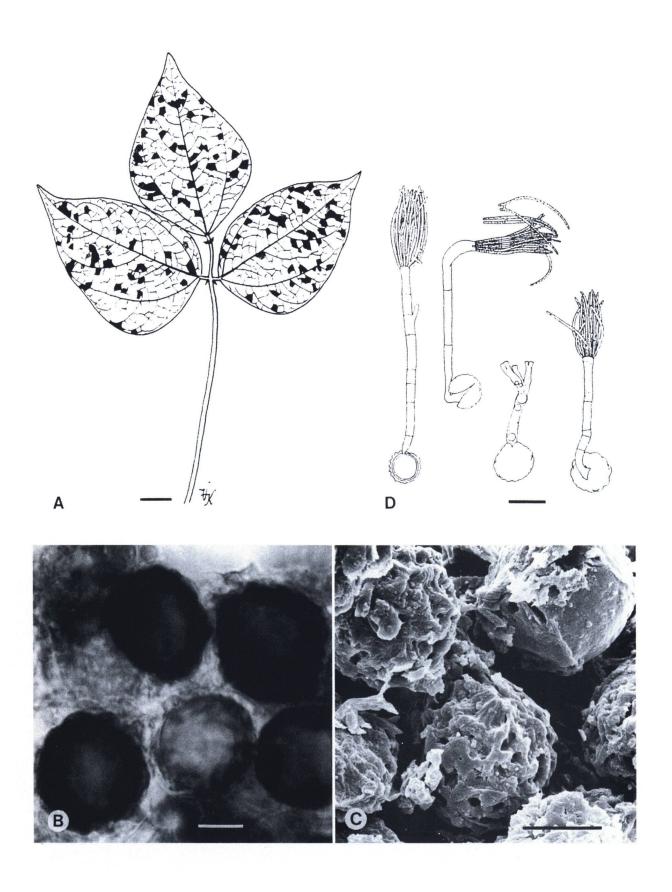
Sori (Fig. 28 A) on leaves forming flat, polyangular, not bursting spots, 2-5(-10) mm in diameter, or larger by fusion, initially pale green, later brown or purplish black with light border. Spores (Figs. 28 B, C) globose, subglobose, ovoid, ellipsoidal, rarely slightly irregular, with a more or less flattened side, (18-)20-27 x (19-)21-30 μm, yellowish to dark reddish brown; wall two-layered, inner layer 1-2 μm thick, outer layer with irregular, rounded or subconical, coarse, 1-3(-5) μm high warts. One or several warts may fuse giving an irregular pattern to the spore surface. Hyphae intercellular, in these the spores develop intercalarly, sometimes terminally, embedded in intercellular spaces of the mesophyll. Spore germination (Fig. 28 D) results in holobasidia bearing numerous, needle-shaped basidiospores which may conjugate.

On Fabaceae: Phaseolus vulgaris L., Vigna mungo (L.) Hepper (Ph. mungo L.), V. radiata (L.) R. Wilczek (Ph. radiatus L.), V. unguiculata (L.) Walp (Ph. unguiculatus L., V. catjang Walp, V. sinensis (L.) Savi ex Hassk.); Africa, S Asia (India), C & S America.

Ref.: Pavgi & Thirumalachar 1953, Joshi 1955, Vakili 1972, 1978, Piepenbring & Bauer 1997, Denchev C. & Denchev T. 2013.

Fig. 28 A-C. Erratomyces patelii on Vigna mungo, Vánky, Ust. exs. no. 1052, HUV 19370.

- A. Sori on a leaf as dark, polyangular, flat spots (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$).
- **D.** Germinating spores (on WA, at room temp., after 1-3 weeks; Bar = $30 \mu m$; after Piepenbring & Bauer 1997:930).



29. *EXOTELIOSPORA* R. Bauer, F. Oberwinkler & K. Vánky, *Mycologia 91*:675, 1999.

Sori on leaves of plants in Osmundaceae (Pteridophyta). *Teliospores* produced in chains on the surface of the host plant. *Host-parasite interaction* by coralloid haustoria in the epidermal cells. *Septal pore* simple, with membrane caps, inner membranous plates are lacking.

Exoteliospora, currently a unispecific genus, belongs to the Melanotaeniaceae. It is one of the very few smut fungi parasitizing lower, flowerless plants (ferns; comp. also *Melaniella*). *Type of the genus*:

Exoteliospora osmundae (H.C. Peck) R. Bauer, F. Oberwinkler & K. Vánky, *Mycologia 91*:675, 1999.

Ustilago osmundae Peck, Bot. Gaz. (Crawfordsville) 6:276, 1881. — Mycosyrinx osmundae (Peck) Peck, New York State Mus. Bull. 157:43, 1912. — Type on Osmunda regalis, USA, Vermont State, 27.VII.1880, leg. C.G. Pringle 1541, NY.

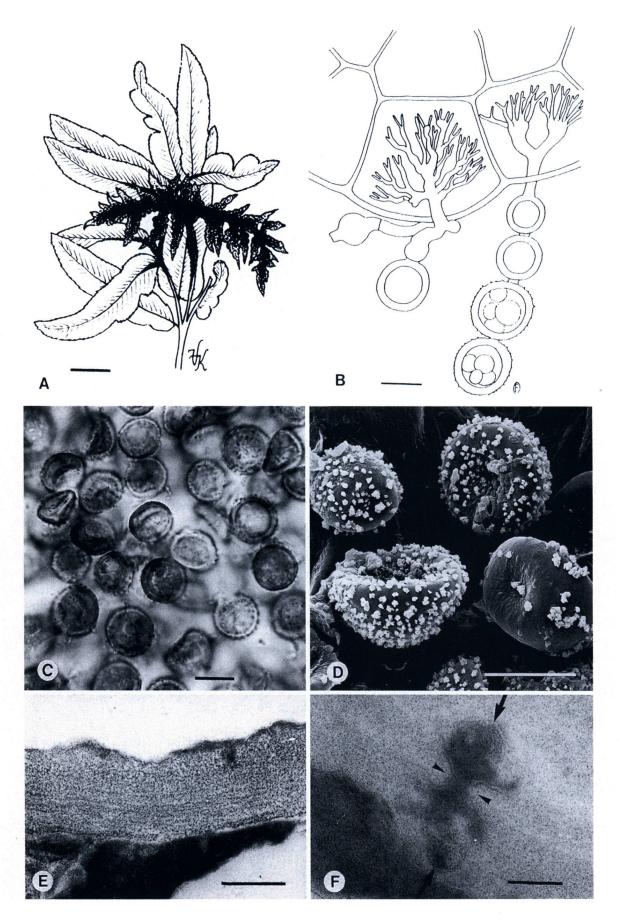
Mycosyrinx osmundae (Peck) Peck var. osmundae-cinnamomea Peck, New York State Mus. Bull. 157:43, 1912 (as 'Mycosyrinx osmundae cinnamomeae'). — Type on Osmunda cinnamomea, USA, Washington Co., Cambridge, 17.VI.1911, leg. S.H. Burnham, NY. (Syn. by Vánky 2007a:56).

Sori (Figs. 29 A, B) external on both sides of deformed and hypertrophied leaves, covering them with a cinnamon- to reddish brown layer of sporogenous hyphae and spores produced in chains (Fig. 29 B). Spores (Figs. 29 C, D) varying in size and ornamentation, globose, subglobose, rarely ellipsoidal, 9-18(-23) x 10-19(-23) μm, pale yellowish- to orange-brown; wall 1-1.5 μm thick, smooth to prominently verrucose. Spore germination unknown. Host-parasite interaction (Fig. 29 B) by coralloid haustoria penetrating into the epidermal cells. Septal pore (Fig. 29 F) simple, with lips not swollen and with membrane caps, inner membranous plates are lacking.

On Osmundaceae (Pteridophyta): Osmunda cinnamomea L., O. regalis L., O. regalis var. spectabilis (Willd.) A. Gray; N America (Canada, USA).

Ref.: Peck 1881, 1912, Bauer, Oberwinkler & Vánky 1999.

- **Fig. 29 A-F.** *Exoteliospora osmundae* on *Osmunda regalis*, USA, New York, Herkimer Co, N of Cedarville, Thuja swamp, 7.VIII.1958, S.J. Smith 26619, H.A. Jamnback & G.E. Larson, HUV 13596, ex NY.
- A. Sori in the deformed, darker leaves. Habit (Bar = 1 cm).
- **B.** T.S. through a sorus showing coralloid haustoria in epidermal cells and the mode of sporogenesis (Bauer *et al.* 1999:670, fig. 2).
- C, D. Spores in LM and in SEM (Bars 10 µm).
- **E.** Section through a hypha in TEM, showing the fibrillate structure of the wall, typical for a basidiomycete (Bar = $0.2 \mu m$, photo R. Bauer).
- **F.** Septal pore in a sporogenous hypha in TEM, with rounded pore lips (arrow heads) and two membrane caps (arrows; Bar = $0.1 \mu m$; photo R. Bauer).



30. FARYSIA M. Raciborski.

Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math. Nat., 1909:354, 1909.

ELATEROMYCES Bubák, Houby České 2:32, 1912. — Type: E. olivaceus (DC.) Bubák (= Farysia thuemenii) on Carex riparia Curtis, France.

Sori in single flowers (ovaries or ovarial pedicels) of Cyperaceae (Carex, Uncinia) species, when young covered by a fungal peridium which bursts at maturity disclosing the olivaceous to dark brown, dusty or semi-agglutinated spore mass traversed by numerous, conspicuous, capillitium-like fascicles of sterile hyphae functioning as elaters. Spores single, small, varying in shape and size, ornamented, pigmented (brown), produced in chains by the division of the sporogenous hyphae. Spore germination results in a short basidium on which several cylindrical or spindle-shaped basidiospores are formed. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Septa poreless.

Farysia, in the Anthracoideaceae, order Ustilaginales, has c. 20 known species. Their delimitation is difficult due to the great variability of the shape and size of the spores, even within the same sorus. A critical revision of the genus is missing. Type of the genus: Farysia javanica Racib. (= F. butleri).

Farysia butleri (H. & P. Sydow) H. & P. Sydow, Ann. Mycol. 17:42, 1919.

Ustilago butleri H. & P. Sydow, in H. & P. Sydow & Butler, Ann. Mycol. 4:424, 1906. — Type on "Scleria elata Thw." (= misnamed Carex filicina, det. Vánky), India, Assam, Thuria, 16.V.1905, leg. E.J. Butler 549, S.

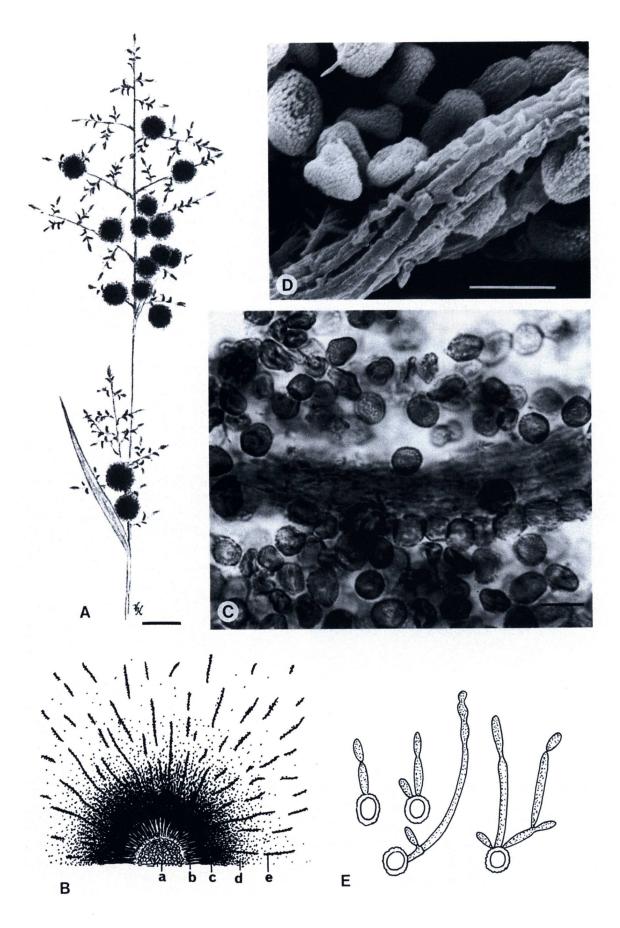
For synonyms as *Cintractia merrillii* Henn., *Farysia javanica* Racib., *F. backeri* Cif., *F. caricis-filicinae* S. Ito, *F. ugandana* Zundel, see Vánky, *Smut Fungi of the World*, 2011('2012'):228.

Sori (Figs. 30 A, B) in some flowers of an inflorescence, initially as small, ovoid to cylindrical bodies, concealed by the perigynium, covered by a grayish white to pale brown peridium, soon bursting, the peridium becomes shredded and the mature sorus exposed with the olive-brown, dusty spore mass traversed by numerous, prominent fascicles of radially arranged hyphae. *Spores* (Figs. 30 C, D) rather varying in shape and size, globose, subglobose, ovoid, broadly ellipsoidal, rarely pyriform, irregularly rounded polyangular or elongate, (5-)6-9 x 6-10.5 μm, olivaceous brown, finely but distinctly, densely verruculose, warts often arranged in short rows, spore profile wavy to finely serrulate, in SEM the surface is provided with truncate or rounded, very densely arranged, sometimes confluent, c. 0.3 μm high warts. Spores formed in chains by the division of the sporogenous hyphae arising from a basal stroma. Other mycelia, originating also from the stroma, remain sterile and form the characteristic, capillitium-like elaters. These fascicles are composed of few to many, parallel, adherent, septate, pale olivaceous brown mycelia, playing an active role in the liberation of the spores from the sori. *Spore germination* (Fig. 30 E) results in a short basidium which buds off several ovoid, cylindrical or fusiform basidiospores in rows or branches (Brefeld 1883, Yen 1937).

On Cyperaceae, *Carex* (subgen. *Indocarex*), on c. eleven *Carex* species; Africa, S & SE Asia, Indonesia, Philippines, Australasia (PNG).

Ref.: Sydow H. & P. 1919, Fischer E. 1920, Liro 1938, Ciferri 1933, Cunningham 1945a, Thirumalachar 1950a, Nannfeldt in Lindeberg 1959, Vánky 2009d, Vánky & Begerow 2007.

- Fig. 30 A-D. Farysia butleri on Carex filicina. A, B. Vánky, Ust. exs. no. 346, HUV 10720. C, D, type.
- A. Sori in some ovaries of an inflorescence. Habit (Bar = 1 cm). B. T.S. of a sorus. (a) = host tissue permeated by hyphae, (b) = hyphal fascicles, (c) = spores and fascicles of sterile hyphae (elaters) in differentiation, (d) = mature spores, (e) = fascicles of sterile hyphae with spores on their surface. C, D. Spores and fascicles of sterile hyphae in LM and in SEM (Bars = $10 \mu m$).
- E. Spore germination of Farysia thuemenii (A.A. Fisch. Waldh.) Nannf. on Carex riparia (after Yen 1937:340).



31. FARYSPORIUM K. Vánky,

Mycotaxon 71:208, 1999.

Sori surrounding the pedicels, peduncles and main axes of the inflorescence of Cyperaceae (Gahnia) forming black, agglutinated to granular or granular-powdery mass of spore balls and spores mixed with fascicles of sterile hyphae (elaters), columella and peridium absent. Spores in loose spore balls or single, pigmented. Spores and fascicles of sterile hyphae differentiating from a fungal stroma on the surface of the host tissues. Sterile cells between or within the spore balls lacking. Spore germination results in either septate basidia or in long filaments. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Farysporium is a unispecific genus, placed tentatively into the Anthracoideaceae. Type of the genus:

Farysporium endotrichum (M.J. Berkeley) K. Vánky,

Mycotaxon 71:208, 1999.

Ustilago endotricha Berk., in Hooker, Fl. Novae Zelandiae 2:196, 1855. — Farysia endotricha (Berk.) H. & P. Sydow, Ann. Mycol. 17:41, 1919. — Elateromyces endotrichus (Berk.) Cunningham, Trans. & Proc. New Zealand Inst. 55:416, 1924. — Type on Gahnia sp., New Zealand, Auckland, leg. A. Sinclair, K.

Sori (Figs. 31 A, B) surrounding the pedicels and main axes of the inflorescence (sometimes only partly), only rarely in the flowers, fusiform, ellipsoidal or globoid, 0.3-1(-2) x 0.5-4(-7) cm, black or blackish brown, composed of compact spore masses with a powdery surface, traversed by numerous, radially arranged fascicles of sterile hyphae that extend beyond the spore masses. Peridium on the surface of young sori was not observed. At maturity, the spore mass breaks into small pieces composed of agglutinated spore balls and single spores. Spore balls (Figs. 31 C, D) ellipsoidal or irregular, 20-50 µm long, dark olivaceous- or chestnut-brown, composed of (2-)3-15(-20 or more?) easily separating spores. Spores (Figs. 31 C, D) globose, subglobose, ellipsoidal, pyriform or irregular, (11-)12-17 x 13-19 µm, olivaceous to chestnut-brown; wall 2-3 µm thick including the typically cracked (scaly) exospore, sometimes with a short, hyaline papilla at one end. Spore formation at the basal part of the sori in radially arranged sporogenous hyphae (Fig. 31 B). Immature spores fusiform, in chains, yellow, thick-walled, smooth, becoming larger, ellipsoidal or globose, pigmented, with a cracked exospore, agglutinated in balls and often with one or several slightly flattened sides. Capillitium-like fungal filaments (elaters) between the spore masses arise from the basal stroma, are 10-50 μm wide, up to 15 mm long, yellowish- to dark olivaceous brown, composed of numerous, agglutinated, elongate, transversally septate, 1.5-2.5 µm wide hyphae, apparently without cell content. Spore germination (Fig. 31 E; of freshly collected spores, in water, at room temp., after 5 days) resulted in either septate basidia or in long hyphae. Basidia giving rise to hyphae or to shorter or longer, fusiform basidiospores that separate easily (Vánky 1997b:153, fig. 2).

On Cyperaceae: *Gahnia grandis* (Labill.) S.T. Blake, *G. pauciflora* T. Kirk, *G. procera* J.R. & G. Forst., *G. setifolia* (A. Rich.) Hook. fil., *G. xanthocarpa* (Hook. fil.) Hook. fil.; Australia, New Zealand.

Ref.: Sydow H. & P. 1919, Vánky 1997b, 1999c.

Fig. 31 A-E. Farysporium endotrichum on Gahnia species. New Zealand.

- **A.** Sori around the pedicels, peduncles and main axes of the inflorescence of *Gahnia procera*. Habit (HUV 18722; Bar = 1 cm).
- **B.** T.S. of a part of a sorus, with host plant tissue (h), and fungal stroma (s) from which spore balls and strands of sterile hyphae (capillitia) develop. (HUV 10573; Bar = $100 \mu m$).
- **C, D.** Spore balls and spores, with typically cracked surface, in LM and in SEM. In SEM picture also a part of a capillitium is seen (HUV 10573; Bars = $10 \mu m$).
- E. Germinating spores from G. setifolia (A. Rich.) Hook. fil. (HUV 14950; Bar = 10 μm).



32. *FLAMINGOMYCES* R. Bauer, M. Lutz, M. Piątek, K. Vánky & F. Oberwinkler, *Mycol. Res.* 111:1202, 2007.

Sori on host plants in Ruppiaceae (Ruppia), dark, not pulverulent. Spores embedded in the host tissue, single, pigmented (yellowish brown, without violet or reddish tint). Spore germination results in hyphae. Host-parasite interaction by intracellular, aseptate haustoria with an electron opaque vesicular matrix coating the haustorial cell wall. Septal pore simple, with two outer tripartite membrane caps and two inner non-membranous plates.

Flamingomyces is a unispecific genus in the Urocystidaceae. Type of the genus:

Flamingomyces ruppiae (G. Feldmann-Mazoyer) R. Bauer, M. Lutz, M. Piątek, K. Vánky & F. Oberwinkler, *Mycol. Res.* 111:1203, 2007.

Melanotaenium ruppiae Feldmann-Mazoyer, Rev. Gen. Bot. 66:36, 1959. — Type on Ruppia maritima, France, Dépt. Pyrénées-Orientales, "rive orientale de l'étang du Canet", 28.V.1958, leg. C. Abelard, in Herb. G. Viennot-Bourgin, PC; isotype HUV 12904!

Sori (Fig. 32 B) in basal part of the leaves and in rhizomes as blackish brown, swollen striae, $0.3-0.5 \times 2-10$ mm, or larger by confluence, with spores embedded in the lacunae of the host tissue. Spores (Figs. 32 C, D) subglobose, ovoid, ellipsoidal, elongate or more or less irregular, often with 1(-2) subacute or acute tips, 9-14.5 \times 10.5-19(-23) μ m, yellowish brown; wall even, 0.5-0.8 μ m thick, smooth. Spore germination (Fig. 32 E) results in hyphae.

On Ruppiaceae: Ruppia maritima L.; S Europe (France).

Ref.: Feldmann-Mazoyer 1959, Bauer, Lutz, Piątek, Vánky & Oberwinkler 2007.

Fig. 32 A-D. Flamingomyces ruppiae on Ruppia maritima, isotype, HUV 12904.

- **A.** Part of a healthy plant.
- **B.** Sori on basal part of the leaves. Habit (Bar = 1 cm).
- **C, D.** Spores in LM and in SEM (Bars = $10 \mu m$).
- E. Spore germination (on WA, at room temp., in a few days; after Bauer et al. 2007:1202; Bar = 10 μm).



33. *FLOROMYCES* K. Vánky, M. Lutz & R. Bauer, *Mycotaxon*, *104*:175, 2008.

Sori on host plants in Agavaceae (Liliaceae s. lat.), forming a blackish brown, powdery mass of spore balls in the flowers. Peridium, columella and sterile cells lacking. Infection systemic. Spore balls permanent, composed of spores only. Spores pigmented (olivaceous- or reddish brown, without violet, orange or rusty color). Spore germination results in both septate and non-septate basidia and also in ramifying, non-septate hyphae. Basidiospores usually septate, produced on sterigmata, germinating by secondary sporidia or by hyphae. Host-parasite interaction by haustoria. Septal pore simple. Type of the genus: F. anemarrhenae.

Floromyces is currently a unispecific genus in the Floromycetaceae within the order Urocystidales.

Floromyces anemarrhenae (C.H. Chow & Chi C. Chang) K. Vánky, M. Lutz & R. Bauer, Mycotaxon 104:175, 2008.

Thecaphora anemarrhenae C.H. Chow & Chi C. Chang, Acta Microbiol. Sin. 14:161, 1974. — Type on Anemarrhena asphodeloides, China, Liaoning Prov., Tungling, Shenyang, 'in Instituto Investigationis Pharmacopaeiae Provinciae Liaoning', 20.VI.1963, leg. C.H. Chow & & C.C. Chang, HMAS 35509; isotype HUV 12007!

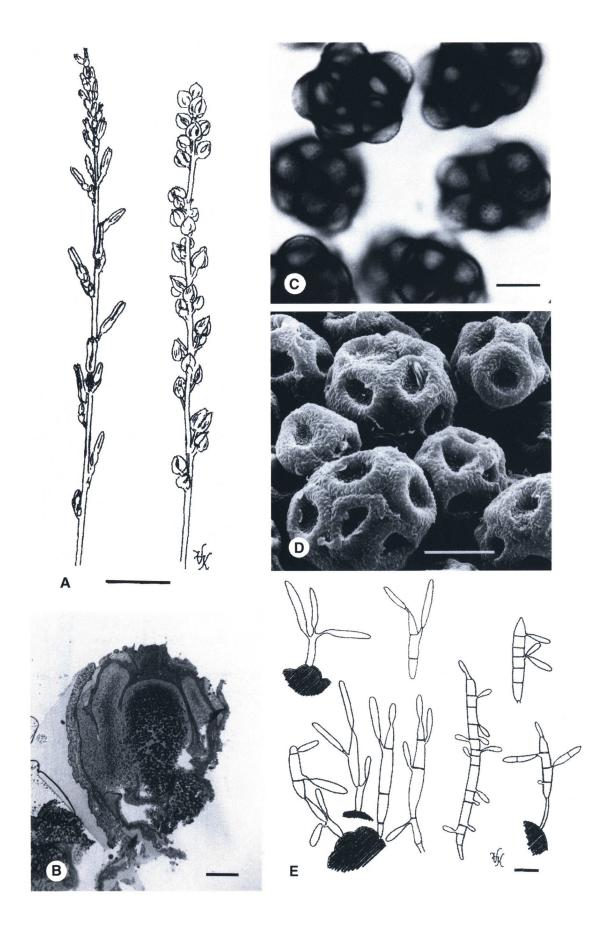
Sori (Figs. 33 A, B) in all flowers of an inflorescence, in the inner floral organs including gynoecium, enclosed by the hypertrophied perianth, filled with blackish brown, powdery mass of spore balls. Peridium, columella and sterile cells lacking. Infected inflorescence shortened. Spore balls (Figs. 33 C, D) globose, subglobose, ellipsoidal to slightly irregular, 16-45 × 20-60 µm, olive-brown, composed of 6-20 (or more?) firmly united spores which rupture rather than separate by strong pressure. Spores (Figs. 33 C, D) broadly subcuneiform, in surface view rounded subpolygonally irregular, rarely circular or elliptic, 9-13 × 9-16 μm, radially 8-15 µm long, olive-brown; wall on the flattened contact sides 1-2 µm thick, smooth, that on the convex, free surface 1.5-3 µm thick, finely, densely, uniformly verruculose which just affects the spore profile. The spore balls differentiate within a hyaline mass of sporogenous hyphae. In this mass appear initially small, scattered groups of mycelia with short, filamentous protoplasm, without a concentric arrangement. These become swollen, increase in size whereas the surrounding hyaline fungal mass is gradually consumed and disappears. Finally, mature spore balls are filling the middle of the sori whereas spore balls are still developing on the surface of the host tissue. Spore germination (Fig. 33 E; Vánky et al. 2008b:177) results in long-ellipsoidal, broadly fusiform or cylindrical, (2-)3-8(-14)-celled phragmobasidia, 2.5-4 × 8-26 μm, usually on a narrow, shorter or longer pedicel. On the basidia, laterally and apically basidiospores are produced on well-developed sterigmata. Spore germination may result also in short holobasidia, producing apically a few, long-ellipsoidal basidiospores on sterigmata. Spores may germinate also by long, aseptate or sparsely septate hyphae. Mature basidiospores (1-)2(-3)-celled, long ellipsoidal or broadly fusiform, 2.5-4 × 8-26 μm, giving rise to secondary sporidia or to hyphae. No conjugation of basidial cells or basidiospores was observed.

On Agavaceae (Liliaceae s. lat.): Anemarrhena asphodeloides Bunge; C & E Asia (China).

Ref.: Chow & Chang 1974, Vánky, Lutz & Bauer 2008b.

Fig. 33 A-D. Floromyces anemarrhenae on Anemarrhena asphodeloides, isotype, HUV 12007.

- **A.** Sori in all flowers of an inflorescence. Healthy inflorescence (left).
- **B.** L.S. of a sorus (Bar = $200 \mu m$).
- C, D. Spore balls and spores in LM and in SEM.
- **E.** Spore germination (on water, at room temp., in 12 hours) resulting in both septate and non-septate basidia and also in ramifying, non-septate hyphae. Basidiospores usually septate, produced on sterigmata, germinating by secondary sporidia or by hyphae; Vánky, Ust. exs. no. 1303, HUV 21738 (Bar = $10 \mu m$).



34. *FRANZPETRAKIA* M.J. Thirumalachar & M.S. Pavgi, in Pavgi & Thirumalachar, *Sydowia, Beih., 1*:(2), 1957, emend. Guo, Vánky & Mordue, *Mycosystema 3*:58, 1990.

Sori in the inflorescence of Poaceae, composed of a central columella of host tissue, numerous long, slender, fragile chains of sterile fungal cells, and a dusty spore mass. Chains of sterile cells arising from the columella are fixed at their proximal end to the columella and are free at their distal end. Spores single, dark-colored. Spore germination results in phragmobasidia. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Franzpetrakia belongs to the Ustilaginaceae. The genus was studied by Guo, Vánky & Mordue (1990). Three species of Franzpetrakia are known: 1. F. okudairae (Miyabe) L. Guo, Vánky & Mordue on Coix lacryma-jobi L. from China and Japan, 2. F. phaceluri Vánky, R.G. Shivas & L. Guo on Phacelurus latifolius (Steud.) Ohwi from China, and 3. The type of the genus:

Franzpetrakia microstegii M.J. Thirumalachar & M.S. Pavgi,

in Pavgi & Thirumalachar, Sydowia, Beih., 1:(2), 1957 (as "microstegiae").

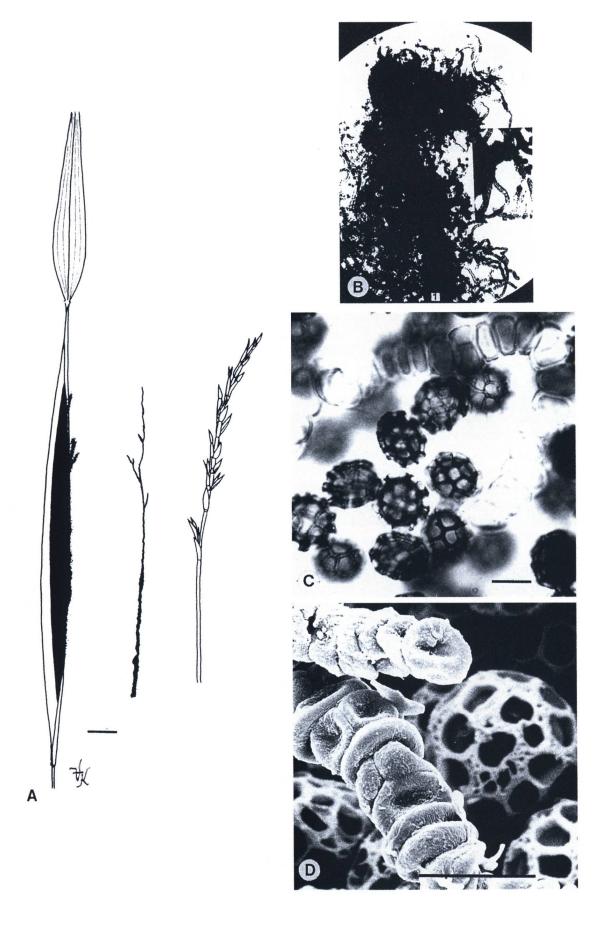
Type on *Microstegium* ('*Microstegia*') sp., India, Uttar Pradesh, Mussoorie Hills, "Mossy Fall", IX.1954, leg. M.S. Pavgi (Type not found).

Sori (Figs. 34 A, B) destroying the entire inflorescence, fusiform, 5-10 cm long, c. 0.5 cm wide, initially concealed by the uppermost leaf-sheath, later protruding as dark brown, powdery mass of spores mixed with numerous slender, filiform chains of sterile fungal cells surrounding a central, ramified columella of host origin. Infection systemic; all shoots of a plant affected. *Spores* (Figs. 34 C, D) globose, subglobose, ellipsoidal, 10-15 × 12-16 μm, olive-brown, reticulate, meshes polyangular or subpolyangular, complete, rarely incomplete, (2-)3-5 per spore diam., muri c. 0.5 μm wide, (1-)1.5-2.5(-3) μm high, with a rounded tip, 10-16 on the spore circumference, in SEM muri smooth or with minute, irregular reticulations in groups, mainly at the angles. *Chains of sterile cells* (Figs. 34 B, C, D) several mm long, 5.5-11 μm wide, composed of a single row of fungal cells. Individual cells (Figs. 34 C, D) variable in form and size, oblong with both ends truncate, subtetrahederal or subglobose, 3-7 × 5.5-7(-11) μm, subhyaline to pale yellowish brown tinted; wall slightly uneven, 0.5-1(-1.5) μm thick, apparently smooth, in SEM rough to finely low verruculose. *Spore germination* (Pavgi & Thirumalachar 1957:3) results in septate basidium laterally and terminally bearing hyaline, ellipsoidal basidiospores, 2.5 × 6-9 μm.

On Poaceae: Microstegium vagans (Nees ex Steud.) A. Camus, Microstegium sp.; S & SE Asia (India, Thailand).

Ref.: Pavgi & Thirumalachar 1957, Guo, Vánky & Mordue 1990, Vánky 2007.

- Fig. 34 A, C, D. Franzpetrakia phaceluri on Phacelurus latifolius, China, Yunnan Prov., Kunming, Hot Spring, 28.IX.1987, L. Guo, HUV 13861. B. Franzpetrakia microstegii on Microstegium sp., type.
- **A.** A sorus, partly hidden by the uppermost leaf sheath (left), a naked columella (middle) and a healthy inflorescence (right).
- **B.** A columella with the attached, long chains of fungal cells. The spores have been removed by washing (after Pavgi & Thirumalachar 1957).
- C, D. Spores and chains of sterile cells in LM and in SEM.



35. *FULVISPORIUM* K. Vánky, in Vánky, Bauer & Begerow, *Mycotaxon 64*:59, 29.IX.1997.

Sori in vegetative tissues of Poaceae in which spore balls are produced intercellularly. No peridium, no columella, no groups of sterile cells between the spore balls. Spore balls permanent, weakly pigmented (pale golden-yellow), composed of spores only. Spore germination of Ustilago-type. Host-parasite interaction by intercellular hyphae lacking interactions with deposits of specific fungal vesicles. Septal pore simple lacking caps. Type of the genus: F. restifaciens.

Fulvisporium is a unispecific genus, belonging to the Ustilentylomataceae of the Microbotryales.

Fulvisporium restifaciens (D.E. Shaw) K. Vánky,

in Vánky, Bauer & Begerow, Mycotaxon 64:59, 1997.

Tolyposporium restifaciens D.E. Shaw, Proc. Linn. Soc. New South Wales 77:145, 1952. — Sorosporium restifaciens (D.E. Shaw) Thirumalachar & Neergaard, Friesia 11:185, 1978('1977'). — Type on Stipa aristiglumis (= Austrostipa aristiglumis), Australia, New South Wales, Breeza Plains, 10.XII.1951, leg. G. Dickson, SYD 693; isotypes IMI 47686, HUV 17795!

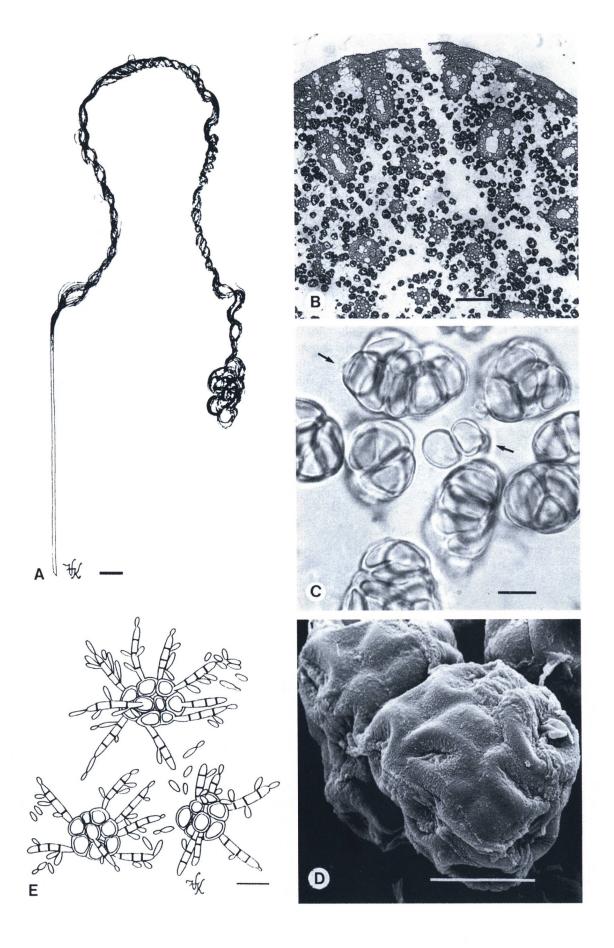
Sori (Figs. 35 A, B) in distal internode(s) of stems, when mature resembling twisted, teased-out ropes, 0.5-1 cm wide, 20-50(-90) cm long, consisting of vascular bundles and a yellowish brown, later cinnamon brown, granular-powdery mass of spore balls, replacing the destroyed intervascular parenchymatic tissue. Spore balls (Figs. 35 C, D) subglobose, broadly ellipsoidal, ovoid, often elongate or slightly irregular, (10-)13-32 x (12-)16-40(-55) μm, golden-yellow to pale yellowish brown, translucent, composed of (1-)5-25 (or more?) firmly united spores. Spores (Figs. 35 C, D) varying in shape and size, rounded with flattened contact sides, from ovoid, ellipsoidal, elongate, hemiglobose to subpolyhedrally irregular, 6-12(-13) x 8-14(-16) μm, pale golden-yellow; wall smooth, 1-2(-3) μm thick, thinner on the contact sides, thicker at the angles. In the center of the free surface the exospore is thin forming a round, c. 2 μm wide germ pore that protrudes slightly in rehydrated spores forming a small papilla, in dehydrated spores it is depressed. In young stages, sporogenous hyphae grow between the cells of the stem parenchyma. Later, thin-walled, hyaline spore ball initials are formed between the parenchyma cells, these increase in size, become thick-walled and slightly pigmented. At maturity, the epidermis ruptures releasing the spore masses. In old sori, the remaining, naked vascular bundles appeare as teased-out ropes. Spore germination (Fig. 35 E) results in 4-celled basidia measuring 2-3(-4) x 15-25(-28) μm. On the basidia, laterally and terminally, ovoid or long-ellipsoidal, sessile basidiospores are produced measuring 1.5-2 x 4-8 μm.

On Poaceae: Austrostipa aristiglumis (F. Muell.) S.W.L. Jacobs & J. Everett (Stipa aristiglumis F. Muell.), A. bigeniculata (Hughes) S.W.L. Jacobs & J. Everett (S. bigeniculata Hughes), A. blackii (C.E. Hubb.) S.W.L. Jacobs & J. Everett (S. blackii C.E. Hubb.), A. rudis (Spreng.) S.W.L. Jacobs & J. Everett (S. rudis Spreng.), A. scabra (Lindl) S.W.L. Jacobs & J. Everett subsp. falcata (Hughes) S.W.L. Jacobs & J. Everett (S. falcata Hughes), A. setacea (R.Br.) S.W.L. Jacobs & J. Everett (S. setacea R.Br.), A. stuposa (Hughes) S.W.L. Jacobs & J. Everett (S. stuposa Hughes), A. variabilis (Hughes) S.W.L. Jacobs & J. Everett (S. variabilis Hughes), Austrostipa sp.; Australia.

Ref.: Shaw 1952, Vánky, Bauer & Begerow 1997.

Fig. 35 A-E. *Fulvisporium restifaciens* on *Austrostipa stuposa*, Australia, Tasmania, 5.III.1996, leg. C. & K. Vánky, HUV 17637.

- **A.** A sorus on the distal part of a culm as teased-out rope. Habit (Bar = 1 cm).
- **B.** T.S. of a sorus with spore balls in the intervascular parenchymatic tissues (Bar = 100 µm).
- C, D. Spore balls and spores in LM and in SEM. In the rehydrated spores, the germ pore protrudes (fig. C, arrows).
- **E.** Spore germination (on MYP, at room temp., after 1-2 days) resulting in 4-celled basidia with ovoid to long-ellipsoidal, sessile basidiospores.



36. GEMINAGO K. Vánky & R. Bauer,

in Vánky, Mycoscience 37:182, 1996.

Sori in cavities of hypertrophied host tissue of plants in Sterculiaceae. Spore mass dark, powdery. Spores in pairs, pigmented (brown). Spore germination results in phragmobasidia. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Type of the genus: G. nonveilleri.

Geminago is a unispecific genus in the Geminaginaceae of the order Ustilaginales. Its type species, G. nonveilleri, is one of the very few smut fungi that parasitize woody plants, namely trees, Triplochiton scleroxylon, in the Sterculiaceae (comp also Pericladium and Uleiella).

Geminago nonveilleri (C. Zambettakis & J. Foko) K. Vánky & R. Bauer,

in Vánky, Mycoscience 37:183, 1996.

Mycosyrinx nonveilleri Zambettakis & Foko, Rev. Mycol. (Paris) 35:304, 1971. — Type on Triplochiton scleroxylon, Central Africa, Cameroon, Yaoundé, 1970, leg. G. Nonveiller, PC; isotype HUV 1449!

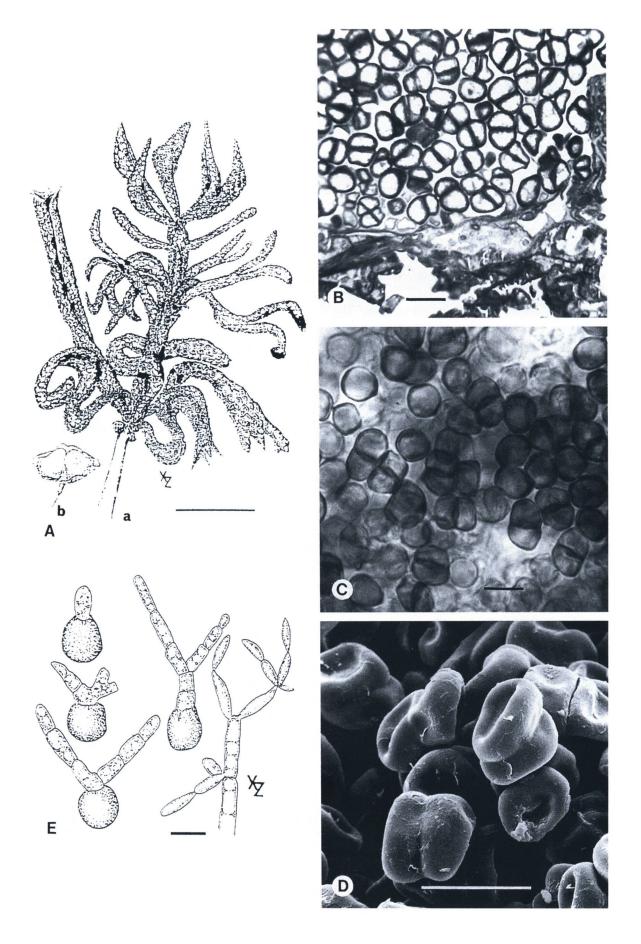
Sori (Figs. 36 A, B) in all floral parts, considerably hypertrophied and deformed, with dark brown, semipowdery spore mass produced centripetally in globoid, ovoid or irregular cavities of 1-2 x 1.5-4 mm, embedded in superficial layers of the host tissue which later rupture disclosing the spores. With maturation the sorus surface becomes spotted, initially by a few, scattered, blackish brown dots, the opened cavities. These are lined by sporogenous hyphae and filled with spores. Later the spots increase in number giving the sorus surface a peculiar, alveolar pattern, resembling an irregular honeycomb. The floral bud is susceptible to direct infection (Zambettakis & Foko 1971). Spores (Figs. 36 B, C, D) in pairs, adhering on the whole flattened surface of the spores, later they may separate partially or completely. Single spores in side view hemispherical or somewhat irregular with a flattened side, 5-7(-8) μm wide, in plane view circular or slightly irregular, 7-9.5 x 7-10.5 μm, olive-brown; wall uneven, 1-2 μm thick, smooth. In TEM (Fig. 36 B), the paired spores are tightly adhering. The outer, electron-dense layer of the spore wall is considerably thickened towards the center of the adhering surface and, at high magnification, shows a peculiar, irregular, radial pattern of medium electron density. The hyphal wall has a finely layered, fibrillar structure indicating also that the fungus is a basidiomycete. Spore germination (Fig. 36 E) results in septate, ramified basidia composed of variable numbers of cells. On the basidia, ovoid, elongate, fusiform, brown basidiospores are produced in chains or in groups, laterally or terminally (Zambettakis & Foko 1971, Ofong 1978). In cultures short-celled hyphae were observed producing "sporidia" at the edge of colonies and large, thick-walled, dark brown chlamydospores in chains towards the center of the colonies (Ofong & Okafo 1980).

On Sterculiaceae: Triplochiton scleroxylon K. Schum.; Central Africa (Cameroon, Ivory Coast, Nigeria).

Ref.: Zambettakis & Foko 1971, Ofong 1978, Ofong & Okafo 1980, Vánky 1996b.

Fig. 36 A-D. Geminago nonveilleri on Triplochiton scleroxylon, isotype, HUV 1149.

- **A.** (a) Sori in a hypertrophied and strongly deformed flower, and (b) a healthy flower (reproduced from Zambettakis & Foko 1971:293; Bar = 5 cm).
- **B.** T.S. of a sorus in TEM.
- **C, D.** Pairs of spores in LM and in SEM.
- **E.** Germinating spores (after Zambettakis & Foko 1971).



37. GEORGEFISCHERIA M.J. Thirumalachar & M.J. Narasimhan, in Narasimhan, Thirumalachar, Srinivasan & Govindu, *Mycologia* 55:33, 1963, emend. Raghunath, *Nova Hedwigia* 21:267, 1972('1971'), emend. Gandhe, in Patil & Gandhe, *Maharashtra Vidnyan Mandir Patrika* 15:87, 1980.

Sori on host plants in Convolvulaceae, foli- or caulicolous, systemic, causing hypertrophy and witches' brooms or yellowing of leaves and blackening of veins. Spore mass dark (brown), agglutinated, not bursting. Spores pale yellowish to olive-brown, globoid to ovoid. Spore wall thick, multilayered, with gelatinized outer layers. Spore germination results in holobasidia on which an apical whorl of 2-4, ellipsoidal to cylindrical basidiospores is produced. These germinate by hyphae and also by ballistospores. Host-parasite interaction apparatus is lacking, hyphae intercellular (Fig. 1, p. 22). Mature septa poreless. Type of the genus: G. riveae.

Georgefischeria, in the Georgefischeriaceae, has four species, all from India: **1.** G. mundkurii Gandhe on Lettsomia setosa Roxb., **2.** G. narasimhanii S.D. Patil & Gandhe on Argyreia hookeri Clarke, **3.** G. thirumalacharii Gandhe on Lettsomia elliptica (Roth) Wight, and **4.** The type of the genus:

Georgefischeria riveae M.J. Thirumalachar & M.J. Narasimhan, in Narasimhan, Thirumalachar, Srinivasan & Govindu, *Mycologia 55*:34, 1963.

Type on *Rivea hypocrateriformis*, India, Poona, XII.1960, leg. M.J. Narasimhan 1260, HCIO, IMI, US. Topotypes: on 17.XI.1961, leg. S.D. Patil, HUV 17513!; I.1968, leg. T. Raghunath, HUV 5369; 22.X.1992, leg. R.V. Gandhe, C. & K. Vánky, HUV 15614!

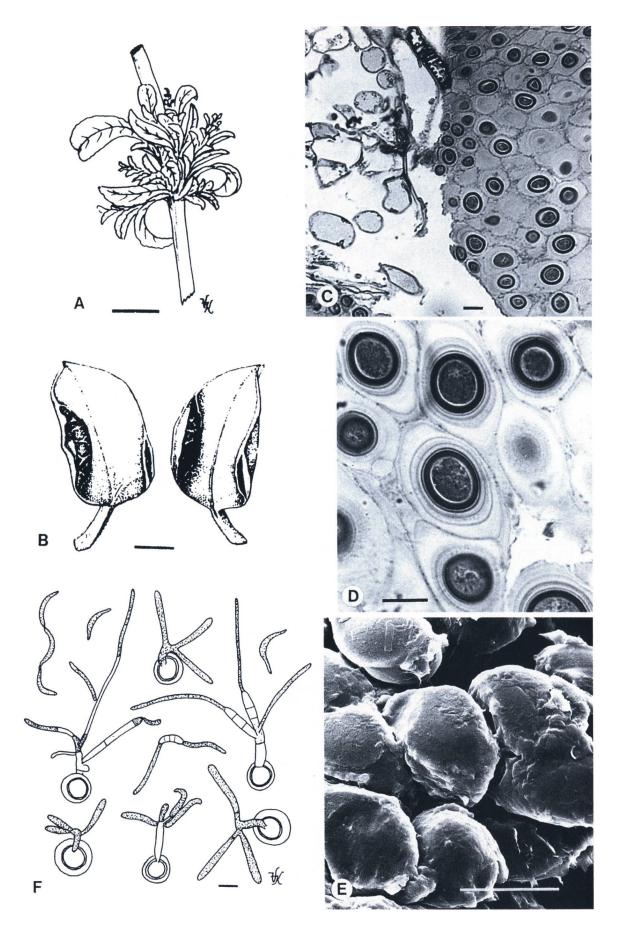
The fungus causing witches' brooms on the axillary shoots (Fig. 37 A), with short internodes and small leaves. *Sori* in leaves (Figs. 37 A, B), stems and fruits. In leaves, sori initially appear as pale yellow patches later turning dark and dry. Infection systemic. Spore mass (Fig. 37 C) embedded in the host tissue, in lysigenous cavities between the two layers of lamina, forming agglutinated, never powdery, many-spored groups. Infected leaves split from their margin, gradually separate in two laminar layers. The lower epidermal layer rolls upwards discharging the spore mass (Raghunath 1967:299), or the infected leaves become dried and irregularly fragmented. *Spores* (Figs. 37 C, D, E) globose, subglobose, ovoid to slightly irregular, 9.5-16 x 10-22.5 μm (without the outer, gelatinous layers), pale yellowish brown to light olive-brown, contents homogeneous or finely granular; pigmented wall slightly uneven, 1.5-3(-4) μm thick, outermost, hyaline layer varying in thickness, gelatinous, gluing the spores together. *Spore germination* (Fig. 37 F) results in a short holobasidium bearing apically a whorl of 2-4 ellipsoidal to cylindrical basidiospores which germinate by hyphae and also by ballistospores (comp. also Narasimhan *et al.* 1963:33, and Raghunath 1969b:224). Ballistospores (Fig. 36 F) slightly bent, allantoid, with subacute tips, 2-4 x 8-18 μm, germinate at one or both ends by filaments or by secondary ballistospores.

On Convolvulaceae: Argyreia cuneata Ker Gawl., Rivea hypocrateriformis Chois.; S Asia (India).

Ref.: Narasimhan, Thirumalachar, Srinivasan, & Govindu 1963, Narasimhan, Thirumalachar & Srinivasan 1964, Raghunath 1967, 1969b, 1972('1971'), Patil & Gandhe 1973, 1980, Bauer, Begerow, Nagler & Oberwinkler 2001.

Fig. 37 A-F. Georgefischeria riveae. A, B. on Argyreia cuneata, C-F. on Rivea hypocrateriformis.

A. Sori on *Argyreia cuneata* forming witches' brooms (India, Poona, Bhugaon, 26.VI.1976, C.H. Phadke, HUV 5370 ex AMH 3162.). **B.** Dried host leaf showing the two layers of laminar tissue rolling apart from the margin exposing the teliospores (Bar = 2.5 mm; after Raghunath 1967:299). **C, D.** T.S. of a sorus in LM, with the spore mass embedded in the host tissue. Note the thick, multilayered, hyaline walls that glue the spores together (India, Poona, I.1968, T. Raghunath, HUV 5369 ex AMH 546). **E.** Spores in SEM of the same material. **F.** Spore germination (on WA at room temp., in 6 days; India, Poona, 22.X.1992, R.V. Gandhe, C. & K. Vánky, HUV 15614; R. Bauer).



38. *GJAERUMIA* R. Bauer, M. Lutz & F. Oberwinkler, *Mycol. Res. 109*:1257, 2005.

Sori forming dark-colored leaf spots on plants in Liliaceae s. lat. Spores single, embedded in the host tissue, pigmented (pale brown, without red or violet tint). Spore germination results in holobasidia bearing an apical whorl of basidiospores producing ballistoconidia. Septal pore is a dolipore.

Gjaerumia, in the Gjaerumiaceae of the order Georgefischeriales, has three known species: **1.** G. eremuri (Schwarzman) Vánky, on Eremurus spp., in C Asia, **2.** G. muscari (Pass. ex J. Schröter) Vánky, on Muscari comosum, Italy, and **3.** The type of the genus:

Gjaerumia ossifragi (E. Rostrup) R. Bauer, M. Lutz & F. Oberwinkler, *Mycol. Res. 109*:1257, 2005.

Entyloma ossifragi Rostrup, Festskr. Bot. Foren. Kjöbenhavn 1890:133, 1890. — Type on Narthecium ossifragum, Denmark, Jylland, Silkeborg, Vesterskov, 17.IX.1885, leg. E. Rostrup, C.

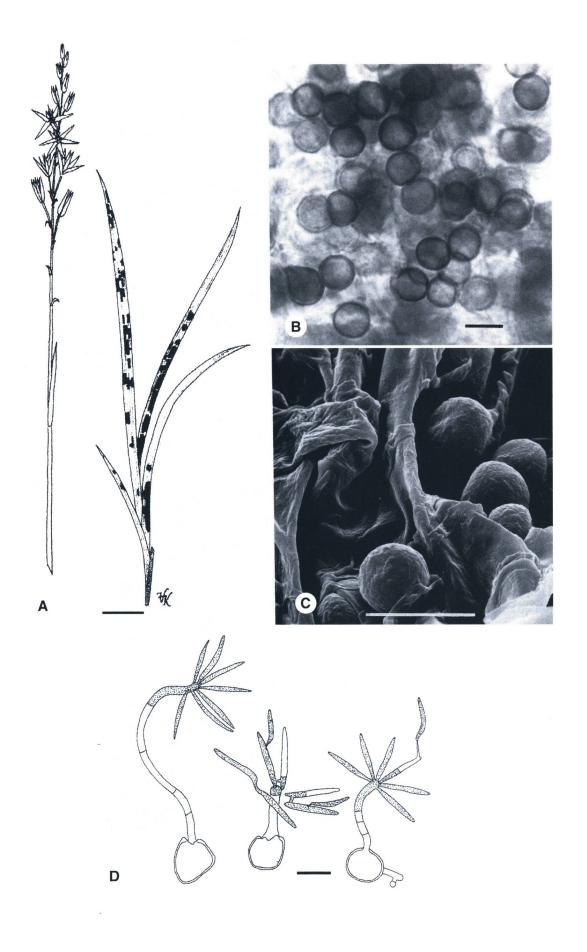
Sori (Fig. 38 A) in leaves and leaf sheaths as grayish black, rectangular to circular spots, delimited by veins, from a few mm to several cm long by fusion. Spores (Figs. 38 B, C) globose, subglobose to irregular by mutual pressure, 9-13 × 10-14.5(-17) μm, light olivaceous brown; wall 1-1.5 μm thick, often with a more or less evident papilla or appendage, in LM smooth to slightly undulate, in SEM with low, rounded warts. Spore germination (Fig. 38 D; Bauer et al. 2005:1255) results in holobasidia bearing an apical whorl of (c. 6) basidiospores that may conjugate producing ballistoconidia. Anamorph absent.

On Melanthiaceae (Liliaceae s. lat.): Narthecium ossifragum (L.) Hudson; N Europe.

Ref.: Bauer, Lutz & Oberwinkler 2005, Vánky 2008:161-162.

Fig. 38 A-C. Gjaerumia ossifragi on Narthecium ossifragum, Vánky, Ust. exs. no. 1187, HUV 20441.

- A. Sori on leaves as grayish black spots. Healthy inflorescence (left).
- B, C. Spores in LM and in SEM.
- **D.** Germinating spores (on WA, at room temp., in a few days; after Bauer et al. 2005:1255; Bar = $10 \mu m$).



39. HETERODOASSANSIA K. Vánky,

Mycotaxon 48:28, 1993.

Sori in leaves, petioles and stems of paludal or aquatic plants (in both mono- and dicotyledonous families), forming pale green, yellowish or brownish areas with numerous spore balls embedded in the host tissue appearing as minute, brown dots. Spore balls rather persistent, consisting of a central mass of spores surrounded by a cortex of sterile cells. Cortex composed of an external layer of small, smooth, empty sterile cells and an internal layer of larger, empty cells with ornamented inner surface. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore simple, with two membrane caps.

Heterodoassansia is similar to Doassansia Cornu, from which it differs by the heterogeneity of the cortex of the spore balls. It belongs to the Doassansiaceae, together with Burrillia, Doassansia, Entylomaster, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudodoassansia, Pseudotracya and Tracya, characterized by complex spore balls, similar ultrastructure and aquatic or paludal host plants. Eight species of Heterodoassansia are known parasitizing both mono- and dicotyledonous plants: 1. H. callitrichis (Jackson & Linder) Vánky (on Callitriche, Callitrichaceae) from USA, 2. H. downingiae (Liro) Vánky (on Downingia, Campanulaceae) from USA, 3. H. hottoniae (Rostr.) Vánky (on Hottonia, Primulaceae) from Europe, 4. H. hygrophilae (Thirum.) Vánky (on Hygrophila, Acanthaceae) from NE Africa, S Asia, 5. H. khandalensis (S.D. Patil & Gandhe) Vánky (on Hemiadelphis, Acanthaceae) from S Asia, 6. H. punctiformis (G. Winter) Vánky (on Lythrum, Lythraceae) from Europe and Australia, 7. H. ranunculina (Davis) Vánky (on Ranunculus, Ranunculaceae) from Europe, N & S America, and 8. The type of the genus:

Heterodoassansia morotiana (G.L. Zundel) K. Vánky,

Mycotaxon 48:28, 1993.

Doassansia morotiana Zundel, Mycologia 43:269, 1951 (nom. nov.). — Doassansia intermedia Morot, J. Bot. (Morot) 9:471, 1895 (not Setchell 1894). — Type on Echinodorus ranunculoides (= Baldellia ranunculoides), France, Maine-et-Loire, Cholet, VIII.1894, leg. C. Morot, PC!

Sori (Fig. 39 A) as leaf spots in which the spore balls appear as small, dark brown, scattered or gregarious, punctiform elevations. Spore balls (Fig. 39 B) globose, mostly 80-135 μm in diameter, composed of a central mass of spores surrounded by a cortex of sterile cells arranged in two layers. Spores (Fig. 39 B) globose, ovoid, ellipsoidal or slightly irregular, 8-11 x 9-13(-15) μm, yellow tinted, thin-walled (c. 0.5 μm), smooth. Sterile cells (Fig. 39 B) pale yellowish brown, darker than the spores, varying in shape and size, those from the inner layer usually subcubical to radially elongate, mainly 10-16 μm long; wall c. 0.8 μm thick, the inner surface (toward the empty lumen) finely echinulate or provided with nail-headed warts up to 1 μm height; sterile cells of the outer layer small, 4-8 μm long, often radially flattened, smooth. Spore germination not studied (expected to be Tilletia-type).

On Alismataceae: Baldellia ranunculoides (L.) Parl. (Alisma ranunculoides L.; Echinodorus ranunculoides (L.) Engelm.), Macherocarpus californicus (Torr.) Small (Echinodorus californicus Torr.); Europe, Africa, N America.

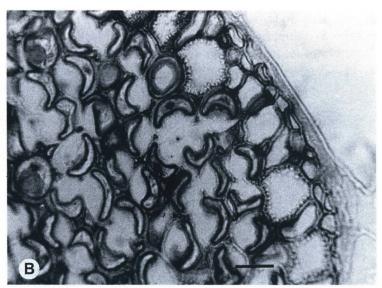
Ref.: Morot 1895, Zundel 1951, Vánky 1993, 1998a.

Fig. 39 A-B. Heterodoassansia morotiana on Baldellia ranunculoides, type, PC.

A. Sori in the leaves.

B. Part of a sectioned and stained spore ball showing the central mass of spores surrounded by a cortex of two kinds of sterile cells. The inner surface of the large, sterile cells of the second layer is finely echinulate. (Spore content often collapsed in this embedded, sectioned and stained specimen, seen in LM).





40. HETEROTOLYPOSPORIUM K. Vánky,

Mycotaxon 63:144, 1997.

Sori in various organs of the host plants in Cyperaceae and Juncaceae, forming naked spore masses consisting of two kinds of spores: thick-walled, pigmented spores, usually agglutinated in spore balls, and thin-walled, smaller, colorless, solitary spores dispersed between the spore balls. Spore balls composed of spores only. No peridium, no columella and sterile cells between the spore balls and spores. Germination of both types of spores resulting in phragmobasidia. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Heterotolyposporium, in the Anthracoideaceae, occurs in the southern hemisphere. It has two known species: H. lepidospermatis on Lepidosperma, and H. piluliforme (Berk.) Vánky on Juncus species. The concomitant presence of two kinds of spores in the sori of Heterotolyposporium is a unique feature within the smut fungi. This is a peculiar kind of adaptation for a more efficient dispersal. The small, easily germinating, hyaline spores enable rapid spread of infection during the summer. The thick-walled, dark, resistant spores ensure survival during adverse winter conditions, starting new infection cycles in the spring (comp. also Conidiosporomyces). Type of the genus:

Heterotolyposporium lepidospermatis K. Vánky,

Mycotaxon 63:144, 1997 (as 'lepidospermae').

Type on *Lepidosperma ensiforme*, Australia, Tasmania, North Coast, 10 km E of Launceston, 41°27′ S 147°14′ E, alt. c. 30 m, 15.III.1996, leg. C. & K. Vánky, HO; isotypes BPI, HUV 17818! and in Vánky, Ust. exs. no. 957.

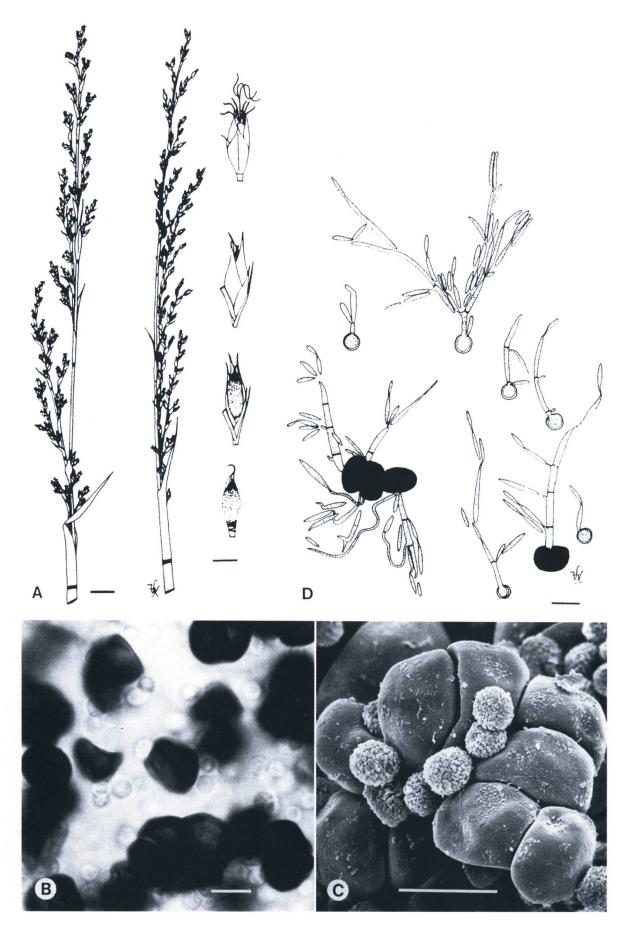
Sori (Fig. 40 A) in all flowers of a panicle, completely hidden by the glumes, c. $1.5 \times 2-2.5$ mm, filling the flowers with a gray to grayish black mixture of dark spore balls and numerous small, hyaline spores (hence the gray color of the spore mass when dry). Spore mass replacing all central floral organs except the outermost 3 or 4 glumes; powdery except for the agglutinated, pointed top and rounded basal part. Spore balls (Figs. 40 B. C) dark reddish brown, ovoid, elongate, usually irregular, rather permanent, comprising 2-10(-25) (or more?) pigmented spores, 15-35(-40) x 18-40(-50) μm, or spores single. Coiled groups of sporogenous hyphae not preceding the formation of spore balls. *Pigmented spores* (Figs. 40 B, C) reddish to dark reddish brown, varying in form, irregular, subpolyhedral or elongate, with flattened contact sides, hemiglobose or hemiovoid, 6.5-15 x 12-20 μm; wall smooth, of variable thickness (0.5-)1-4(-5) μm, thickest at the angles. Hyaline spores (Figs. 40 B, C) between the spore balls numerous, solitary or in groups but not forming balls, globose to broadly ellipsoidal, varying in size, 4-8 x 5-10 µm, hyaline to very pale yellow; wall c. 1 µm thick, in LM finely punctate which does not affect the spore profile, in SEM densely, irregularly verrucose. Germination of the pigmented spores (Fig. 40 D) results in 2-4-celled basidia measuring 2-3 x 15-50 µm. On the basidia, on sterigmata, laterally and terminally, ovoid, long ellipsoidal to subfusiform basidiospores are produced measuring 1-1.5(-2) x 6-15(-20) µm. On the basidia hyphae are also produced which later become septate and ramified. Germination of the hyaline spores (Fig. 40 D) resulting in similar but usually smaller basidia and basidiospores, the basidia often only 2-celled.

On Cyperaceae: Lepidosperma ensiforme (Rodway) D.I. Morris; Australia. Known only from the type collection.

Ref.: Vánky 1997c.

Fig. 40 A-D. Heterotolyposporium lepidospermatis on Lepidosperma ensiforme, isotype, HUV 17818.

- A. Sori in the spikelets. A healthy (left) and an infected panicle (right). Enlarged a healthy (top) and three infected spikelets, with partly and completely removed floral envelopes (Bar for detail drawing = 2 mm).
- **B**, **C**. Pigmented and hyaline spores in LM and in SEM.
- **D.** Germinating pigmented and hyaline spores with 2-4-celled basidia on which, on sterigmata, ovoid, long ellipsoidal basidiospores are produced (on WA, at room temp., after 1-2 days).



41. INGOLDIOMYCES K. Vánky,

in Vánky & Bauer, Mycotaxon 59:279, 1996.

Sori in ovaries of Poaceae, swollen, composed of an outer membrane of host and fungus origin, and a central mass of spores mixed with sterile cells. Columella, groups of conidia between the spores, and smell of trimethylamine of the spore mass absent. Spores solitary, pale colored, ornamented. Spore germination results in aseptate basidia on which apically, on sterigmata, a few, large, bent ballisto-basidiospores are produced. Host-parasite interaction by intercellular hyphae; interaction apparatus is lacking. Septal pore a dolipore traversed by two membranous plates, pore caps lacking. Type of the genus: I. hyalosporus.

The presence of ballisto-basidiospores differentiates this unispecific genus from other genera of the Tilletiaceae. Spore ornamentation is also unique.

Ingoldiomyces hyalosporus (G.E. Massee) K. Vánky,

in Vánky & R. Bauer, Mycotaxon 59:280, 1996.

Tilletia hyalospora Massee, Bull. Misc. Inform. 1899:148, 1899. — Type on Piptochaetium sp. (= Nassella pubiflora), Bolivian Andes, near Sorata, c. 3450 m, leg. G. Mandon, in Plantae Andium Boliv. no. 1275, NY; isotype in S.

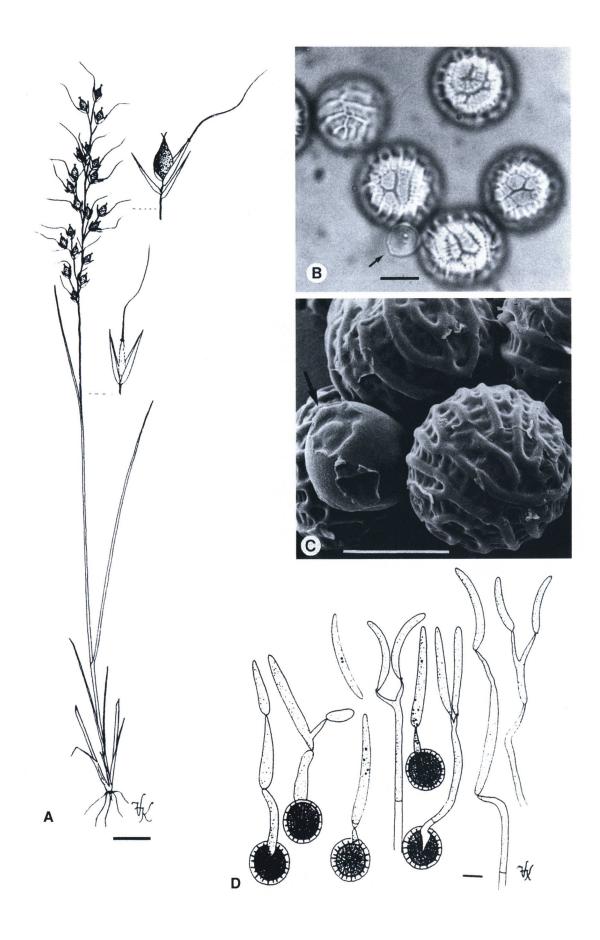
For synonyms as *Tilletia hypsophila* Speg., *Tilletia wilcoxiana* Griffiths, and *Tilletia boliviensis* Liro, see Vánky, *Illustrated genera* 2nd ed., 2002:80.

Sori (Fig. 41 A) in all ovaries of an inflorescence, swollen, ovoid to ellipsoidal with a short, acute tip, 1-2 x 1.5-3 mm, covered by a first green, later brown membrane (pericarp) that ruptures at maturity disclosing the pale yellowish- to reddish brown, semi-powdery mass of spores and sterile cells. Spores (Figs. 41 B, C) solitary, globose, subglobose to ellipsoidal, 16-22 x 18-24 μm, subhyaline to pale yellowish brown; wall 3-5 μm thick, peculiarly ornamented by a few coarse ridges which run parallel on the spore surface, or more commonly ramify and anastomose to form an irregularly reticulated pattern. These coarse ridges are joined by finer, narrow, short, secondary ridges that, in their turn (seen only in LM), may be connected by very fine tertiary ridges. Sterile cells (Figs. 41 B, C) globose, subglobose to ellipsoidal, smaller than the spores (8-14 x 8-16 μm); wall 0.5-3 μm thick, hyaline, smooth. Spore germination (Fig. 41 D) results in aseptate basidia. On the top of basidia, on sterigmata, one or two, bent, hyaline, aerial, ballistosporic basidiospores are produced measuring 5-6.5 x 30-75 μm. (For details and cultural characteristics see Ingold (1995b) and Vánky & Bauer (1996)).

On Poaceae: Nassella caespitosa Griseb. (Stipa caespitosa (Griseb.) Speg.) N. chilensis (Trin. & Rupr.) E. Desv., N. inconspicua (J. Presl) Barkworth (Stipa inconspicua J. Presl), N. mexicana (Hitchc.) Pohl (Stipa mexicana Hitchc.), N. pubiflora (Trin. & Rupr.) E. Desv., Piptochaetium indutum Parodi, P. montevidense (Spreng.) Parodi, P. panicoides (Lam.) E. Desv., Stipa conspicua? J. Presl, S. lepida Hitchc. (S. hassei Vasey; S. eminens Cav. var. andersonii Vasey), S. leptostachya Griseb., S. rupestris? Phil. (S. depauperata? Pilg.), S. tenuissima Trin.; N & S America.

Ref.: Massee 1899, Ingold 1995b, Vánky & Bauer 1996.

- **Fig. 41 A-D.** *Ingoldiomyces hyalosporus.* **A, D** on *Nassella mexicana*, Vánky, Ust. exs. no. 930 (as *Tilletia hyalospora*), HUV 16417, **B, C** on *Nassella pubiflora*, type, NY.
- A. Sori in all ovaries of an infrorescence. Habit (Bar = 1 cm). Enlarged a sorus and a healthy spikelet.
- **B, C.** Spores and sterile cells (arrows) in LM and in SEM (Bars = $10 \mu m$).
- **D.** Spore germination (on WA, at room temp., in 5-6 days; Bar = $10 \mu m$).



42. *JAMESDICKSONIA* M.J. Thirumalachar, M.S. Pavgi & M.M. Payak, *Mycologia 52*:478, 1961('1960'), emend. Raghunath, *Sydowia 23*:104, 1969, emend. Walker & Shivas, *Mycol. Res. 102*:1212, 1998, emend. Bauer, Begerow, Nagler & Oberwinkler, *Mycol. Res. 105*:422, 2001.

Sori in leaves, leaf sheaths and stems of Poaceae and Cyperaceae as black spots or crusts. *Spores* solitary or in groups, not agglutinated in balls, pigmented (olive-brown), embedded in the host tissue or erumpent, not powdery, or occurring on the surface of the host plants and powdery. *Spore germination* results in holobasidia with ballistic basidiospores or secondary ballistospores. Hyphae mostly intercellular. *Host-parasite interaction* by mostly intercellular hyphae, interaction apparatus is lacking. Mature *septa* poreless.

The genus *Jamesdicksonia* was emended several times and its border widened. It belongs to the Georgefischeriaceae, with 16 (+ 6?) known species: *Type of the genus*:

Jamesdicksonia obesa (H. & P. Sydow) M.J. Thirumalachar, M.S. Pavgi & M.M. Payak, Mycologia 52:478, 1961('1960').

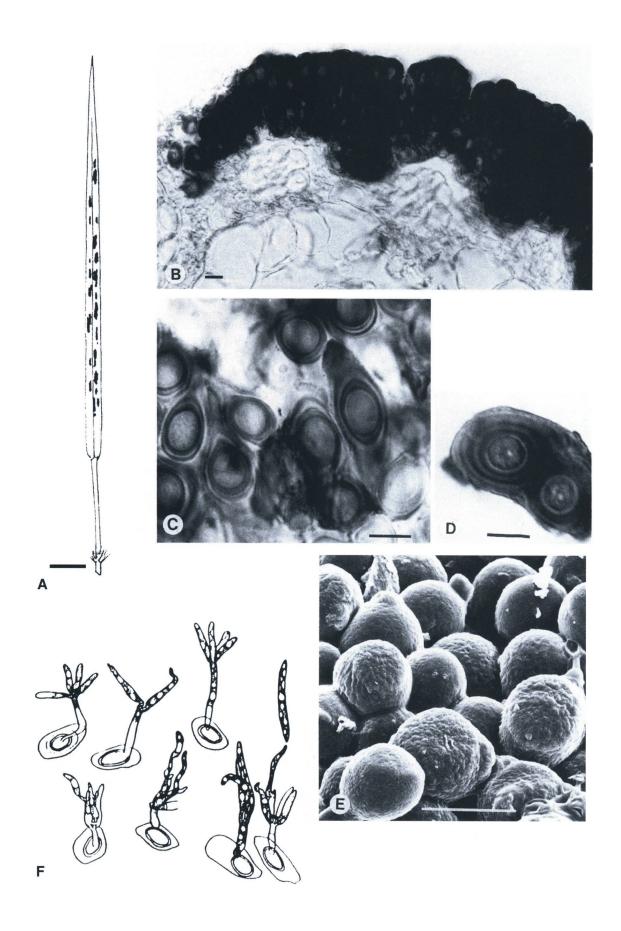
Entyloma obesum H. & P. Sydow, Ann. Mycol. 9:145, 1911. — Tolyposporella obesa (H. & P. Sydow) G.P. Clinton & Zundel, in Zundel, Mycologia 22:157, 1930. — Type on Andropogon annulatus (= Dichanthium annulatum), India, Nagpur, 21.X.1907, leg. P.A. Pundit.

Sori (Figs. 42 A, B) hypophyllous, forming at first subepidermal, later raised and erumpent, hemispherical, hemicylindrical or often fusiform, thick crusts, usually cracked, in T.S. flabelliform, up to 4 mm long, composed of firmly agglutinated spore masses. Spores (Figs. 42 C, D, E) varying in shape and size, globose, ovoid, ellipsoidal, elongate, pyriform, often subpolyhedrally irregular or elongate, 8-11 x 9-13(-15) μm, palw olivaceous to dark reddish brown; wall 3-6.5 μm thick, composed of a homogeneous, thin (0.5-1 μm), uniform endospore and a multilayered, smooth exospore of varying thickness, in SEM spore surface nearly smooth to low verrucose. Spores mature in a basipetal succession in the sorus. Spore germination (Fig. 42 F), without dormancy, results in a holobasidium bearing apically a whorl of 2-4, monokaryotic, haploid basidiospores which conjugate in pairs in situ, and successively bud off dikaryotic, either short, allantoid, crescent-shaped ballistospores or long, cylindrical secondary and tertiary sporidia (Raghunath 1969c).

On Poaceae: Dichanthium annulatum (Forssk.) Stapf (Andropogon annulatus Forssk.), Hyparrhenia rufa (Nees) Stapf; S Asia, S America.

Ref.: Sydow H. & P. 1911b, Zundel 1930, Thirumalachar & Dickson 1949, Thirumalachar, Pavgi & Payak 1961('1960'), Raghunath 1969a, 1969c, 1970, Walker & Shivas 1998, Bauer, Begerow, Nagler & Oberwinkler 2001.

- **Fig. 42 A-F.** *Jamesdicksonia obesa* on *Dichanthium annulatum*. A-E. India, Poona, II.1968, leg. T. Raghunath, HUV 5371 ex AMH 547.
- A. Sori on the abaxial side of a leaf. Habit (Bar = 1 cm).
- **B.** T.S. of a sorus in LM, showing the originally subepidermal, agglutinated spore masses (Bar = $10 \mu m$).
- C, D. Spores in LM, in lactophenol and in water, showing the thick, multilayered structure of the exospore.
- **E.** Spores in SEM (Bars = $10 \mu m$).
- **F.** Spore germination with holobasidia bearing apically 2-4 basidiospores on which allantoid ballistospores and also long sporidia are produced (after Raghunath 1969c:760).



43. *KUNTZEOMYCES* P. Hennings ex P.A. Saccardo & P. Sydow, in Saccardo, *Syll. Fung. 14*:430, 1899.

DIDYMOCHLAMYS Hennings, Hedwigia 36:246, 1897; not Hooker 1872 (Rubiaceae). PERICHLAMYS Henn., in Clements & Shear, The genera of fungi:340, 1931 (nom. nov. superfl.).

Sori in some spikelets in the inflorescence of Cyperaceae (*Rhynchospora*), surrounded by a thick, sac-like, fungal peridium, filled with pigmented (brown) spore masses. *Spores* solitary, large, possessing a peculiar, three-layered wall formed of an exospore and an endospore separated by a hyaline, gelatinous, middle layer. The exospore ruptures releasing the proper spore, covered only by the endospore. *Spore germination* results in phragmobasidia. *Host-parasite interaction* by intracellular hyphae, coated by an electron-opaque matrix. Mature *septa* poreless.

The classification of *Kuntzeomyces* is uncertain. Tentatively it is placed into the Anthracoideaceae. Unique for this genus is the peculiar spore morphology. Two species of *Kuntzeomyces* are known: *K. ruizianae* M. Piepenbr., and the *type of the genus*:

Kuntzeomyces ustilaginoideus (P. Hennings) P. Hennings ex P.A. Saccardo & P. Sydow, in Saccardo, *Syll. Fung. 14*:430, 1899.

Didymochlamys ustilaginoidea Hennings, Hedwigia 36:246, 1897. — Cintractia ustilaginoidea (Henn.) Höhnel, Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 119:879, 1910. — Type on Rhynchospora sp., Brazil, St. Cathar, near Blumenau, leg. E. Ule 1885, FH.

Cintractia occulta Molina-Valero, Caldasia 13:70, 1980. — Type on Rhynchospora sp., Colombia, Dpto. Huila, between La Plata and Puracé, alt. 3150 m, 21.I.1976, leg. L.A. Molina, P. Buriticá, K.P. Dumont & J. Lutein, COL; isotype HUV 8888! (Syn. by Vánky 1987a:52).

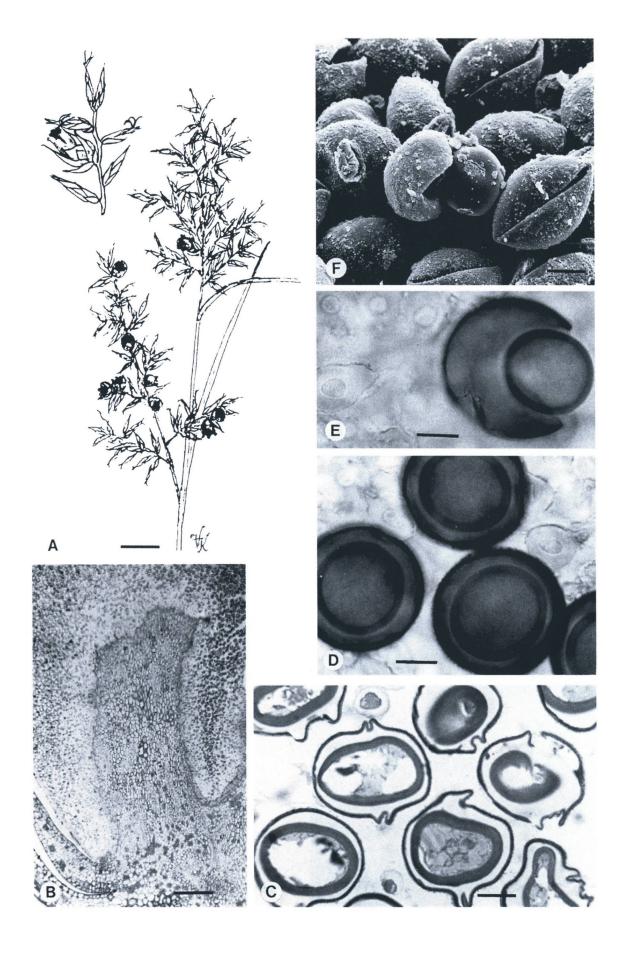
Sori (Fig. 43 A) in some spikelets of the inflorescence, slightly hypertrophied, ovoid, 2-4 x 3-6 mm, initially hidden by the glumes and also covered by a dirty-white to pale brown peridium, later protruding between the glumes and the peridium ruptures irregularly on its apex disclosing the black, agglutinated spore mass. The spore mass develops (Fig. 43 B) on the surface of the aborted floral axis and innermost floral organs. The peridium is composed of a network of longitudinally arranged rows of globose, polyangular, pyriform or fusiform fungal cells, like necklaces of pearls, subhyaline to pale yellow; wall 2.5-7 μm thick. *Spores* (Figs. 43 C-F) globose to subglobose (24-32 x 24-35 μm, with a peculiar wall structure of three layers. The inner layer, the endospore, is uniformly 2-2.5 μm thick, yellow colored, smooth. The middle layer is hyaline, gelatinous, of variable thickness. The outer, membranous layer, the exospore, is finely verruculose, 1-1.5 μm thick, reddish brown, with a long germ slit, where the wall is thinner (c. 0.5 μm) and paler. Under pressure or in humid conditions the exospore ruptures, permitting the true spore, covered only by the endospore, to pass freely (Figs. 43 E, F; comp. also Ling & Stevenson 1949, Piepenbring *et al.* 1998:181). *Spore germination* is not known.

On Cyperaceae: *Rhynchospora hieronymi* Boeck. ssp. *montevidensis* (Barros) Guagl., *R. macrochaeta* Steud. ex Boeck., and *Rhynchospora* sp.; S America.

Ref.: Hennings 1897, Saccardo 1899, Höhnel 1910, Ling & Stevenson 1949, Molina-Valero 1980, Piepenbring, Bauer & Oberwinkler 1998, Piepenbring 2001b.

Fig. 43 A-F. *Kuntzeomyces ustilaginoideus* on *Rhynchospora macrochaeta*. A, B, C, F. Ecuador, 28 km SW of Quito, near San Juan de Chirigallio, alt. c. 3520 m, 4.III.1993, leg. C. & K. Vánky, HUV 17157. D, E. from the isotype of *Cintractia occulta* (= *K. ustilaginoideus*), HUV 8888.

A. Sori in some spikelets. Habit (Bar = 1 cm). Enlarged an infected and some healthy spikelets. **B.** L.S. of the basal part of a young sorus with a central columella of host origin from which sporogenous fungal filaments are growing out producing successively maturing spores (Bar = $100 \mu m$). **C.** T.S. of embedded and colored spores in LM. The wrinkles of the outer layer of the spore wall, on both sides of the thin-walled germ slits, are artifacts through the dehydrated, hyaline middle layer. **D, E, F.** Spores in LM and in SEM. E, F. show a spore passing through the ruptured outer membrane. D, E. also show subhyaline fungal cells of the sorus membrane (Bars = $10 \mu m$).



44. LANGDONIA A.R. McTaggart & R.G. Shivas,

in McTaggart, Shivas, Geering, Vánky & Scharaschkin, Persoonia 29:130, 2012c.

Sori in some or all ovaries of a panicle, infecting hosts of Aristida (Poaceae). Columella absent. Spores usually compacted into spore balls. Sterile cells formed from non-sporogenous hyphae absent. Spore germination of Ustilago-type.

Langdonia, in the Ustilaginaceae, comprises 8 species: 1. L. aristidae (Peck) McTaggart & R.G. Shivas, 2. L. aristidaria (Durán) McTaggart & R.G. Shivas, 3. L. aristidicola (Speg.) McTaggart & R.G. Shivas, 4. L. clandestina (R.G. Shivas, Vánky & Athip.) McTaggart & R.G. Shivas, 5. L. confusa (H.S. Jacks.) McTaggart & R.G. Shivas, 6. L. goniospora (Massee) McTaggart & R.G. Shivas, 7. L. inopinata (Vánky) McTaggart & R.G. Shivas, and 8. The type of the genus:

Langdonia fraseriana (H. Sydow) A.R. McTaggart & R.G. Shivas,

in McTaggart, Shivas, Geering, Vánky & Scharaschkin, Persoonia 29:130, 2012c.

Sorosporium fraserianum H. Sydow, Ann. Mycol. 35:25, 1937. — Sporisorium fraserianum (H. Sydow) Vánky, Mycotaxon 78:308, 2001 — Type on Aristida leptopoda, Australia, New South Wales, Warialda, I.1932, L.R. Fraser 121; isotypes IMI 44415 (ex Univ. of Sydney), isotype HUV 17480!

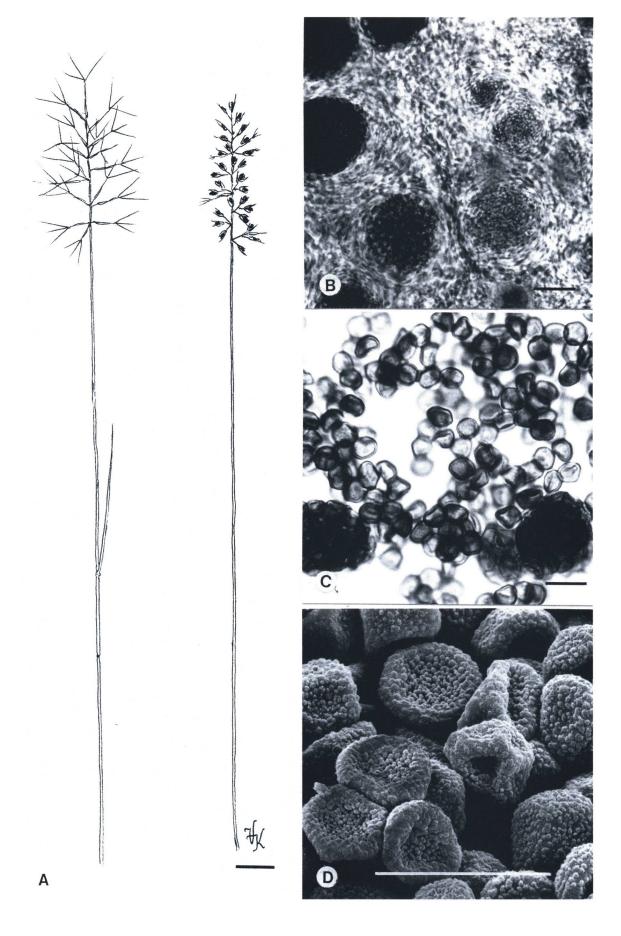
Sori in ovaries, inconspicuous, ovoid or asymmetrically fusiform, $1-1.5 \times 2-6$ mm, partly hidden by the floral envelopes, covered by a first green, later brown pericarp which at maturity ruptures on its sides exposing the blackish brown, powdery mass of spore balls and spores. Usually all ovaries of the inflorescence affected but some ovaries or inflorescence branches may escape infection. Columella and sterile cells lacking. Spore balls irregular, 35-60 μ m or larger, easily disintegrating. Spores globose, subglobose, ellipsoidal or slightly subpolyhedrally irregular, rather uniform in size, $4.5-6(-6.5) \times 5.5-8 \mu$ m, yellowish brown; wall c. 0.5 μ m thick, finely, densely punctate-verruculose, warts usually more pronounced on one side or in a restricted area of the spore surface, spore profile there finely serrulate, the opposite side of the spores almost smooth. Sterile cells absent.

On Poaceae: Aristida caput-medusae Domin, A. contorta F. Muell., A. leptopoda Benth., A. nitidula S.T. Blake ex J.M. Black, A. personata Henrard, A. ramosa R.Br., A. strigosa R.Br., A. vagans Cav.; Australia.

Langdonia fraseriana is close to L. aristidae but in L. fraseriana the spore balls are looser, the spores smaller and less polyhedral than those in L. aristidae.

Ref.: McTaggart, Shivas, Geering, Vánky & Scharaschkin 2012c.

- Fig. 44 A, C, D. Langdonia fraseriana on Aristida leptopoda, isotype, HUV 17480. B. Langdonia consanguinea on A. hygrometrica R. Br., Australia (HUV 19189).
- A. Sori in the ovaries. Habit. To the left a healthy inflorescence (Bar = 1 cm).
- **B.** Spore balls in various developmental stages formed from coiled sporogenous hyphae. (Bar = $25 \mu m$).
- C, D. Spore balls and spores in LM and in SEM; Bars = $10 \mu m$.



45. *LEUCOCINTRACTIA* M. Piepenbring, D. Begerow & F. Oberwinkler, *Mycologia 91*:496, 1999.

Sori around all the pedunculi of an inflorescence or around internodes of the stem of plants in Cyperaceae (Rhynchospora), cylindrical, when young covered by a thick, white peridium that ruptures irregularly disclosing the black, agglutinated spore mass with a powdery surface. Sori with sterile stroma forming sporogenous pockets. Infection systemic. Spores single, flattened, without appendages, covered by irregular, rough warts forming ridges at the sides of the spores. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Type of the genus: L. scleriae.

Ling (1951a) studied *C. leucoderma* and with it related species, including also *C. scleriae* (= Leucocintractia scleriae). In this group, Ling recognized three species and established many synonyms. Piepenbring, Begerow & Oberwinkler (1999) and Piepenbring (2000), based also on molecular analyses, split the genus *Cintractia* into four genera of which one is *Leucocintractia*. Tentatively it is placed into the Anthracoideaceae of the order Ustilaginales. *Leucocintractia* has four recognized species, all on *Rhynchospora*: 1. *L. leucoderma* (Berk.) M. Piepenbr., 2. *L. pachyderma* (H. Sydow) M. Piepenbr., 3. *L. portus-argenti* (Cif.) M. Piepenbr., and 4. The *type of the genus*:

Leucocintractia scleriae (A.P. De Candolle) M. Piepenbring, D. Begerow & F. Oberwinkler, *Mycologia 91*:497, 1999.

Uredo scleriae DC., in Poiret, Encycl. Méth. Bot. 8:228, 1808. — Ustilago scleriae (DC.) Tul. & C. Tulasne, Ann. Sci. Nat. Bot., Sér. 3, 7:89, 1847. — Cintractia scleriae (DC.) L. Ling, Mycologia 43:314, 1951. — Type on Scleria sp. (= Rhynchospora corymbosa (L.) Britton), French Guiana, Cayenne, Herb. De Candolle 555, G.

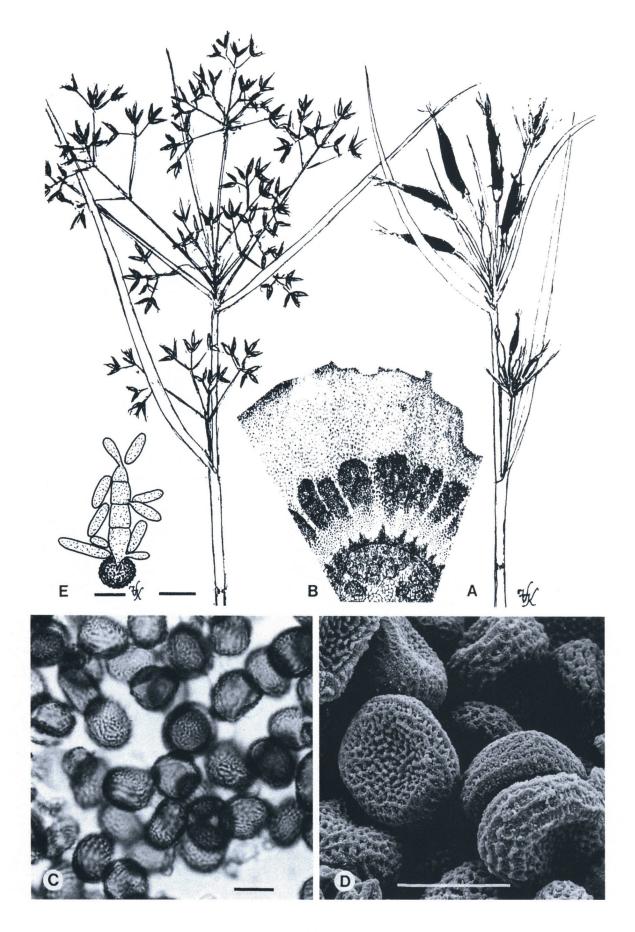
For synonyms as *Cintractia krugiana* Magnus, *C. krugiana* var. *usambarensis* Henn., *Cintractia javanica* Racib., and *Cintractia albida* S. Ito, see Vánky, *Illustrated genera* 2nd ed., 2002:86.

Sori (Figs. 45 A, B) surround all the peduncles of an inflorescence with rudimentary spikelets, cylindrical, often curved, 2-3 x 5-20 mm, at first covered by a thick, white peridium that later ruptures irregularly exposing a black, agglutinated spore mass with a powdery surface. Spores (Figs. 45 C, D) solitary, globose, subglobose or broadly ellipsoidal, (9-)10-15 x (11-)12-16(-17) μm, slightly flattened, 8-12 μm wide, light reddish brown, without appendages; wall 0.5-1 μm thick, covered by irregular, coarse warts and coarse, irregular ridges that are often connected by small, transverse ridges or warts. Spore germination (Fig. 45 E) results in phragmobasidia of which cells are separating readily, producing ellipsoidal basidiospores (comp. also Viégas 1940, as Cintractia leucoderma).

On Cyperaceae: Rhynchospora asperula (Nees) Steud., R. corymbosa (L.) Britton (R. aurea Vahl), R. corniculata (Lam.) A. Gray (R. laxa Vahl), R. gigantea Link, R spectabilis Hochst., R. triflora Vahl, Rhynchospora sp.; cosmopolitan in the tropics.

Ref.: Magnus 1893b, McAlpine 1910, Viégas 1940, Ling 1951a, Piepenbring, Begerow & Oberwinkler 1999, Piepenbring 2000.

- Fig. 45 A-D. Leucocintractia scleriae on Rhynchospora corymbosa, Vánky, Ust. exs. no. 810, HUV 15702.
- A. Sori around all floral peduncles of an inflorescence with aborted spikelets. Healthy inflorescence (left).
- **B.** Part of a T.S. of a sorus (after Magnus 1893b, Pl. 12).
- C, D. Spores in LM and in SEM.
- E. Spore germination (on MYP, at room temp., in 1 day).



46. *LIROA* R. Ciferri,

Nuovo Giorn. Bot. Ital., N.S., 40:263, 1933.

Sori forming irregularly globose swellings in the flowers, on the branches and stems of plants in Polygonaceae (*Polygonum*), in which the spores are produced in lysigenous cavities. Spore mass purplish brown, initially agglutinated, later pulverulent. *Spores* single, pigmented (violet-brown), wall ornamented (finely reticulate), mixed with a "capillitium" of ramified, irregular, rudimentary vascular strands. *Spore germination* results in phragmobasidia on which laterally and terminally, sessile, ovoid basidiospores are produced successively. *Host-parasite interaction* by intercellular hyphae lacking interactions with deposits of specific fungal vesicles. Mature *septa* poreless. *Type of the genus: L. emodensis*.

Liroa is a unispecific genus belonging to the Microbotryaceae.

Liroa emodensis (M.J. Berkeley) R. Ciferri,

Nuovo Giorn. Bot. Ital., N.S., 40:264, 1933.

Ustilago emodensis Berkeley, Hooker's J. Bot. Kew Gard. Misc. 3:202, 1851. — Farysia emodensis (Berk.) H. & P. Sydow, Ann. Mycol. 17:42, 1919. — Melanopsichium emodense (Berk.) Zundel, Ustil. World: 46, 1953. — Microbotryum emodense (Berk.) M. Piepenbring, in Agerer et al. (eds.), Frontiers in Basidiomycote Mycology:159, 2004 (as 'emodensis'). — Type on Polygonum chinense, India, State of West Bengal, Sikkim and Nangki Himalaya, Tonglo (Tonglu), alt. c. 3000 m, leg. W.J. Hooker, K.

Ustilago treubii Solms, Ann. Jard. Bot. (Buitenzorg) 6:79, 1887. — Elateromyces treubii (Solms) Bubák, Arch. Přír. Výzk. Čech. 15(3):33, 1912. — Type on Polygonum chinense, Java, volcano Gedé, Tjibodas, XII.1883, leg. Treub & Solms. (Syn. by H. & P. Sydow 1919:42).

Ustilago rosulata H. & P. Sydow, Ann. Mycol. 10:77, 1912. — Type on Polygonum chinense, Philippines, Luzon, Subprov. Brutoc, V-VI.1910, leg. M. Vanoverberg (E.D. Merrill no. 501). (Syn. by H. & P. Sydow 1919:42; confirmed by Ling 1949:257).

Ustilago lycoperdiformis Zundel, Mycologia 36:402, 1944. — Type on Polygonum sp. (= Polygonum chinense, det. K. Vánky), China, Kwangsi [= Guangsi] Auton. Reg., Ling Yuin Hsien, Loh Hoh Tsuen, 1.IV.1933, leg. S.Y. Cheo 1774, BPI 162794; isotypes BPI 162795, 188939, HUV 13531! (Syn. by Vánky, in Vánky & Oberwinkler 1994:16).

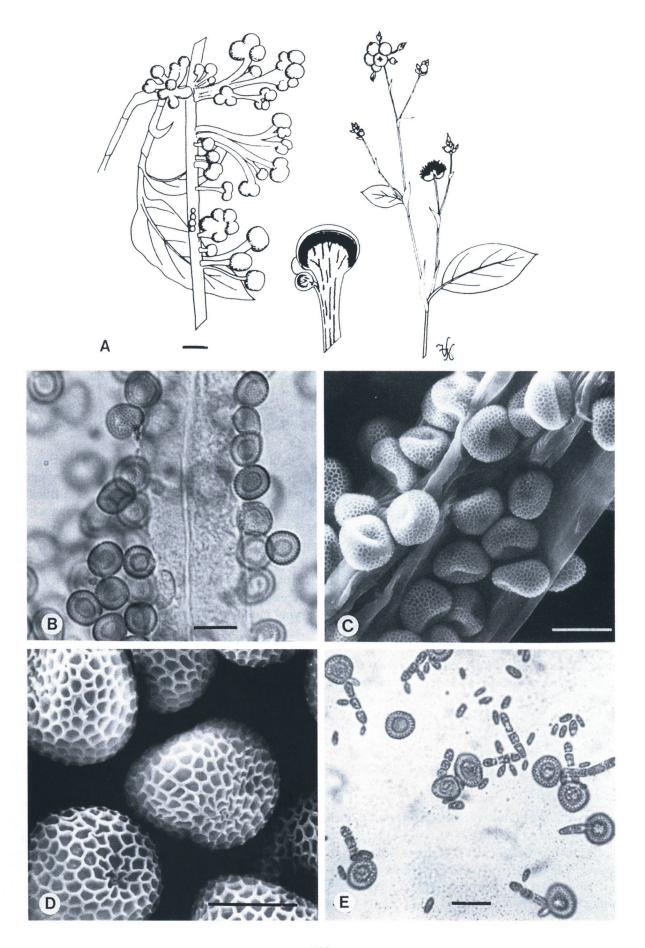
Sori (Fig. 46 A) either on the stems forming large, irregularly globose, stalked swellings, initially green, later purplish brown and hard, or in the swollen, globose flowers. The intercellularly situated sporogenous hyphae are successively and completely transformed into spores, forming semilunate, schizogeneous cavities in the host tissue, filling them with a purplish brown, at first agglutinated, later powdery mass of spores, intermixed with a capillitium of ramified, irregular, rudimentary vascular strands. *Spores* (Figs. 46 B, C, D) globose, subglobose, ovoid to somewhat irregular, (6-)7-8(-9) x 7-10(-11) μm, violet-tinted pale brown, finely and densely reticulate, in SEM irregularly reticulate, 12-16 meshes per spore diameter. *Spore germination* (Fig. 46 E) results usually in a 3-celled basidium (the fourth cell remains in the spore) on which laterally and terminally, sessile, ovoid basidiospores are produced successively, which fuse two by two (Solms 1887:84-85, Pl. IX, figs. 7-9; Viswanathan 1964).

On Polygonaceae: *Polygonum* (sect. *Cephalophilon*), *P. chinense* L.; S & SE Asia, Indonesia, Australasia (PNG).

Ref.: Berkeley 1851, Solms 1887, Bubák 1912, Sydow H. & P. 1912, 1919, Ciferri 1933, Mundkur & Thirumalachar 1946, Ling 1949b, Zundel 1953, Viswanathan 1964, Kamat & Viswanathan 1965, Vánky & Oberwinkler 1994.

Fig. 46 A-E. *Liroa emodensis* on *Polygonum chinense*. A-D. India, Kerala distr., Anamalai Hills, Mt. Anamudi, alt. c. 1900 m, 3.II.1980, leg. K. Vánky, HUV 8905.

A. Sori on the stem and in the flowers. Enlarged, a L.S. of a sorus from the stem, showing the lunate bed of dark spore masses. **B, C, D.** Spores and an "elater" in LM and in SEM. **E.** Germinating spores (on WA, at room temp., in 1 day, HUV 17516).



47. MACALPINOMYCES R.F. Langdon & R.A. Fullerton,

Trans. Brit. Mycol. Soc. 68:30, 1977, emend. Vánky, *Mycotaxon* 59:119, 1996, and *Mycotaxon* 62:129, 1997.

ENDOSPORISORIUM Vánky, Mycotaxon 54:226, 1995. — Type: E. capillipedii (J.N. Mishra) Vánky on Capillipedium parviflorum (R.Br.) Stapf, India. (Syn. by Vánky 1997a:129).

Sori in different organs (ovaries, culms) of host plants in Poaceae, usually producing hypertrophy, covered by a peridium of host tissue permeated by hyphae. True columella lacking. Spores pigmented, tightly packed, usually polyangular, filling the sori. Sterile cells of variable size and wall-thickness, solitary or grouped, hyaline or pale colored, embedded and scattered in the spore mass. At maturity, spore mass disintegrating into irregular groups of variable size or into single spores. Spore germination of Ustilago-type. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

The genus was treated by Vánky (1996a) and its borders widened (Vánky 1996a, 1997a) to include ovaricolous smuts possessing also small sterile cells between the spores, and to include *Endosporisorium* (with sori in the culms or spikelets of the host plants). It is interesting to note that sori of species of *Macalpinomyces*, developed in the ovaries or spikelets, often fall off the plant entirely, whereas similar sori of *Sporisorium* do not fall entirely off the plant; the columella firmly connects the sori with the host plant. *Macalpinomyces*, with 45 known species belongs to the Ustilaginaceae. *Type of the genus*:

Macalpinomyces eriachnes (F. Thümen) R.F.N. Langdon & R.A. Fullerton,

Trans. Brit. Mycol. Soc. 68:30, 1977.

Sorosporium eriachnes Thümen, Flora 61:443, 1878 (as "eriachnis"). — Ustilago australis Cooke, Grevillea 8:34, 1879. — Both names are based on the same collection: Eriachne sp., Australia, Northern Territory, Fitzmaurice River, X.1855, leg. F. von Mueller, HUV 1663!

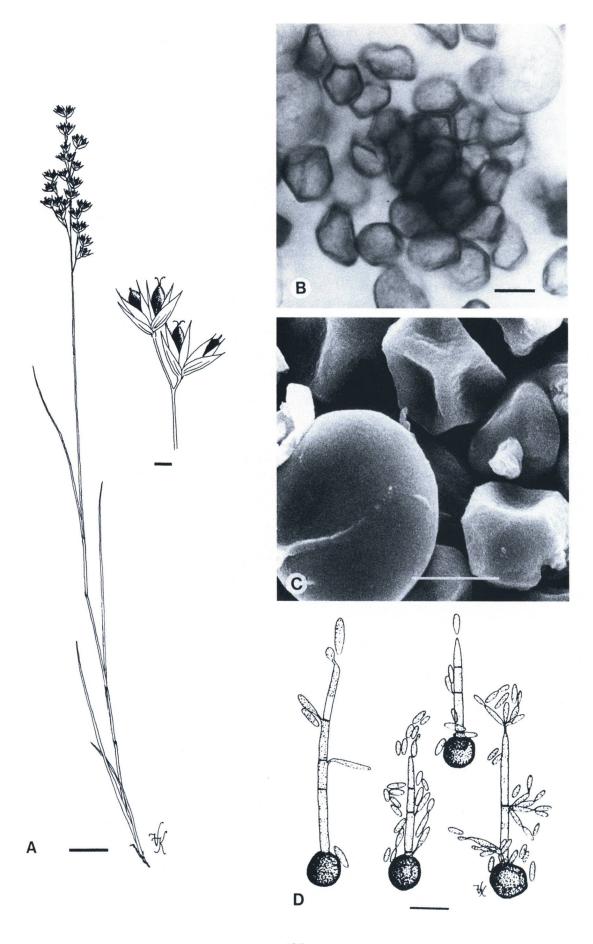
Sori (Fig. 47 A) in all ovaries of an inflorescence, ovoid to ellipsoidal, with a short, acute tip bearing the rest of the stigma, 2-3 x 3-4 mm, covered by a brown peridium composed of the pericarp, permeated by inter- and intracellular hyphae, and a thin, internal layer of hyphae producing the spores and sterile cells. Sori filled with a mass of tightly packed spores in which solitary or grouped giant sterile cells are embedded. Spore mass blackish brown, semi-agglutinated, rather easily disintegrating into irregular, variably large, many-spored groups or into single spores. No columella. Spores (Figs. 47 B, C) mostly polyhedrally or subpolyhedrally irregular, 8-12 x 10-19 μm, cinnamon-brown; wall c. 1 μm thick, smooth or minutely granular. Sterile cells (Figs. 47 B, C) globose, subglobose or slightly irregular, 11-26 x 18-32 μm, pale yellowish brown, contents granular; wall up to 5 μm thick, smooth. Spore germination of hibernated spores resulted partly in simple or branched, septate hyphae partly in 2-4-celled basidia, 1-3 per spore, with varying numbers of fusiform basidiospores arising from each cell (Langdon & Fullerton 1977:29).

On Poaceae: Eriachne agrostidea F. Muell., E. aristidea F. Muell., E. armitii F. Muell. ex Benth., E. avenacea R.Br., E. capillaris R.Br., E. ciliata R.Br., E. festucacea F. Muell. E. glabrata (Mayden) Hartley, E. helmsii Domin, E. melicacea F. Muell., E. mucronata R.Br., E. obtusa R.Br., E. pallescens R.Br. (E. muelleri Domin), E. pauciflora W. Fritzg., E. pulchella Domin, E. pulchella subsp. dominii (Hartley) Lazarides (E. dominii Hartley), E. rara R.Br., E. scleranthoides F. Muell., E. sulcata Hartley, E. triseta Nees, Eriachne sp.; Philippines, Australasia (AU, PNG).

Ref.: Thümen 1878, Cooke 1879, Langdon & Fullerton 1977, Vánky 1995a, 1996a, 1997a, 1997d, 1997e, 1998a, 2000a.

Fig. 47 A-C. Macalpinomyces eriachnes on Eriachne sp., type, HUV 1663.

A. Sori in the ovaries. Habit (Bar = 1 cm). Enlarged some infected ovaries (Bar = 1 mm). **B, C.** Spores and giant sterile cells in LM and in SEM (Bars = 10 μ m). **D.** Germinating spores of *Macalpinomyces eragrostiellae* Vánky & C. Vánky on *Eragrostiellae bifaria* (Vahl) Bor, type. Septate, 4-celled basidia (of which the proximal cell may remain in the spore) produce ovoid to long-ellipsoidal basidiospores on sterigmata, laterally at the septa and terminally (on WA, at 29 °C, in 1 day; Bar = 10 μ m).



48. *MELANIELLA* R. Bauer, K. Vánky, D. Begerow & F. Oberwinkler, *Mycologia 91*:482, 1999.

Sori in leaves or stems of plants in Selaginellaceae (*Selaginella*) forming black, non-erumpent spots. *Spores* single, pigmented (brown), embedded in the host tissue, not pulverulent. Fungal cells exclusively intercellular, hyphae with clamp connections. *Spore germination* of *Exobasidium*-type, i.e. holobasidia with septate, abaxially curved, ballistosporic basidiospores. *Host-parasite interaction* by complex interaction apparatus with cytoplasmic portions. Hyphae intercellular, lacking haustoria. *Septal pore* simple, with membrane caps.

Melaniella belongs to the Melaniellaceae of the order Doassansiales. Two species are known: 1. M. selaginellae (Henn. & E. Nyman) R. Bauer, Vánky, Begerow & Oberw. on Selaginella sp. from Java, and 2. The type of the genus:

Melaniella oreophila (H. Sydow) R. Bauer, K. Vánky, D. Begerow & F. Oberwinkler, Mycologia 91:483, 1999.

Melanotaenium oreophilum H. Sydow, Ann. Mycol. 33:367, 1935. — Neotype (design. by Vánky, in Bauer et al. 1999:483) on Selaginella delicatula (Desv.) Alston (det. Karthikeyan, BSI), India, Uttar Pradesh, Mussoorie, Mt. Gun Hill, alt. c. 2120 m, 20.IX.1992, leg. T. & K. Vánky, HUV 15689!; isoneotypes in Vánky, Ust. exs. no. 912 (as Melanotaenium oreophilum).

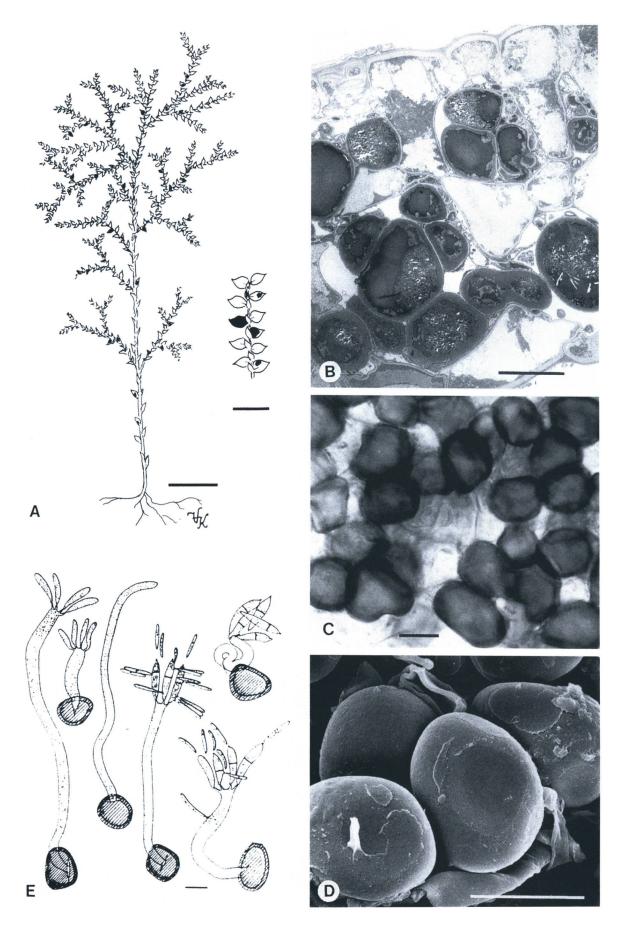
Sori (Figs. 48 A, B) in leaves forming irregular, black spots, 0.1-1(-1.5) mm in diameter, sometimes comprising the entire leaf surface, flat, rarely also in the stems, there up to 20 mm long, non-erumpent. Spores (Figs. 48 B-D) embedded in the host tissue, agglutinated, varying in shape and size, subglobose, ovoid, elongate, usually subpolyhedrally irregular with one or several flattened sides, 12-18 x 13-22(-25) μm, blackish brown; wall two-layered, more or less evenly 1-2 μm thick, smooth. Spore germination (Fig. 48 E) results in 25-120 μm long, proximally 3-4, distally 5-6.5 μm wide holobasidia, apically producing (3-)4(-5) ballistosporic basidiospores, 3-5 x 15-22(-28) μm, with abaxially oriented hilar appendices on well-developed sterigmata. Mature basidiospores two-celled by a transversal septum. Long cylindrical, hyaline, thin-walled, yeast-like cells of 1.5-2 x 10-20 μm are born apically and laterally on the basidiospores, on short sterigmata. The hyphae are intercellular, with clamp connections. In TEM the hyphal wall is electron-opaque, fibrillar.

On Selaginellaceae: Selaginella abyssinica Spring, S. chrysocaula Spring, S. chrysorrhiza Spring, S. delicatula (Desv. ex Poir.) Alston, S. tenera (Hook. fil. & Grev.) Spring, and Selaginella sp.; S Africa (Zimbabwe), S Asia (India). Certainly more widespread but overlooked.

Ref.: Sydow H. 1935, Maheshwari & Puri 1935, Bauer, Vánky, Begerow & Oberwinkler 1999.

Fig. 48 A-E. Melaniella oreophila on Selaginella delicatula, neotype, HUV 15689.

- A. Sori on the leaves. Habit (Bar = 1 cm, that of of detail drawing = 2 mm).
- **B.** T.S. through a sorus with intercellular hyphae and spores in TEM (photo R. Bauer; Bar = $10 \mu m$).
- C, D. Spores in LM and in SEM (Bars = $10 \mu m$).
- **E.** Germinating spores (on WA, at room temp., in one month; R. Bauer), with holobasidia of different stages of maturity. On sterigmata, slightly bent, two-celled ballistosporic basidiospores are produced with their hilar appendages oriented abaxially. On the basidiospores, laterally and terminally, long cylindrical, hyaline, thinwalled, yeast-like cells are born (Bar = $10 \mu m$).



49. MELANOPSICHIUM G. Beck.

Ann. K. K. Naturhist. Hofmus. (Wien) 9:122, 1894.

Sori as conspicuous galls in various parts of host plants in the Polygonaceae (*Polygonum*), composed of hypertrophied host tissue and mycelia, with numerous chambers filled with many, solitary spores embedded in a gelatinous mass. *Spore germination* of *Ustilago*-type. *Host-parasite interaction* by intracellular hyphae, coated by an electron-opaque matrix. Mature *septa* poreless.

Melanopsichium, with two, not sharply delimited species, belongs to the Ustilaginaceae of the order Ustilaginales. The type species, M. austro-americanum, was said to have smooth spores (Spegazzini 1881:64). Mature spores of the type specimen (LPS 3136) studied in LM and in SEM, are more or less finely punctate-verruculose (Vánky 1985a:85). The other species, M. pennsylvanicum Hirschh., has echinulate spores. Several species described as Melanopsichium belong to other genera, or the description was based on wrongly identified host plants (e.g. M. missouriense Whitehead & Thirum. on "Glycine max" is M. pennsylvanicum on Polygonum sp.). Type of the genus:

Melanopsichium austroamericanum (C. Spegazzini) G. Beck,

Ann. K. K. Naturhist. Hofmus. (Wien) 9:122, 1894 (as 'austro-americanum').

Ustilago austroamericana Spegazzini, Anales Soc. Ci. Argent. 12:63, 1881 (as 'austro-americana'). — Sphacelotheca austroamericana (Speg.) Liro, Ann. Acad. Sci. Fenn., Ser. A, 17:150, 1924 (as 'austro-americana'). — Type on Polygonum acre Kunth (= P. punctatum Elliott), Argentina, marshes near Recoleta, V.1881, leg. C. Spegazzini. (On the typewritten label in LPS no. 3136 is written "Melanopsichium austro-americanum (Speg.) Beck, Holotypus. S/ Polygonum acre, Rep. Argentina, Buenos Aires, 8.VIII.1881, leg. C. Spegazzini").

Sori (Figs. 49 A, B) usually in the inflorescence, but also on stems and leaves as conspicuous, purplish black, irregularly lobed galls, elastic when young, viscid when humid, firmly indurate when dry. The galls are composed of hypertrophied host tissue containing numerous, spherical to irregular chambers filled with spores embedded in a hyaline, gelatinous matrix. In humid conditions this gelatinous substance swells considerably and pushes the spore mass out to the sorus surface. *Spores* (Figs. 49 C, D) globose, ovoid to somewhat irregularly elongate, obpyriform, 6-11 x 7.5-15 μm, from pale yellowish brown to pale chestnut-brown; wall 0.7-1 μm thick, smooth to finely punctate-verruculose and with a gelatinous sheath. *Spore germination* (Fig. 49 E) results in one or two, septate basidia on which laterally and terminally ovoid to oblong, hyaline basidiospores are born (Norton 1896 Pl. XXVIII, figs. 9-12, Săvulescu & Manasian 1954:628, fig. 4).

On Polygonaceae: *Polygonum aviculare* L., *P. hydropiper* L. (*P. acre* Lam.), *P. lapathifolium* L., *P. pennsylvanicum* L., *P. punctatum* Elliott (*P. acre* Kunth), *P. virginianum* (L.) Raf.; cosmopolitan.

Due to confusion with M. pennsylvanicum the distribution of this species is uncertain.

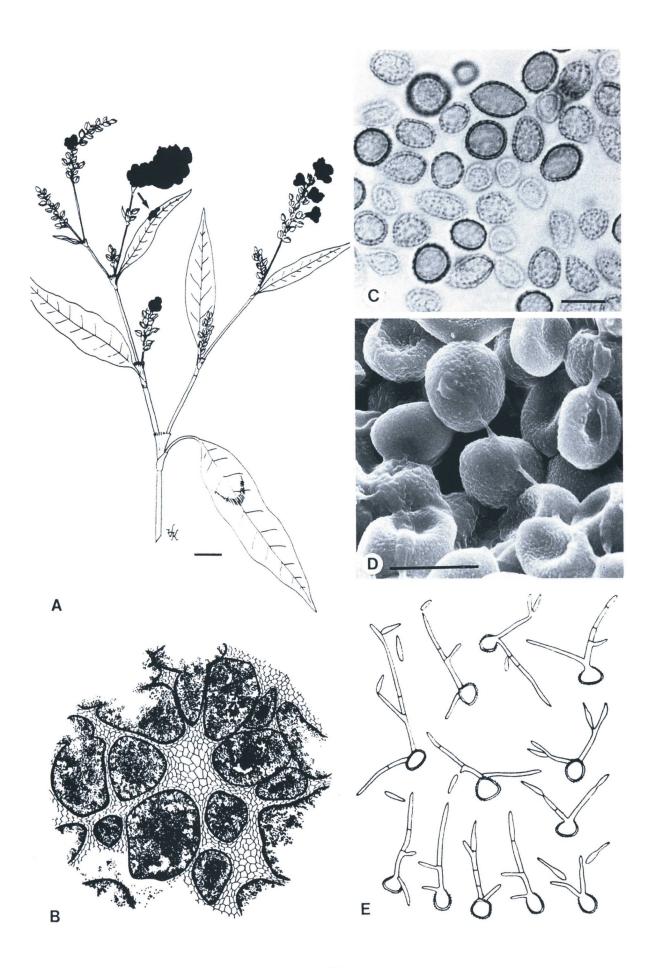
Melanopsichium austro-americanum and *M. pennsylvanicum* are two closely related species producing the same symptoms on the same host plants. They differ only in spore wall ornamentation. Intermediate forms may occur. The two were even merged by Halisky & Barbe (1962).

Ref.: Spegazzini 1881, Beck 1894, Norton 1896, Hirschhorn 1941, Reed 1943, Fischer 1953, Săvulescu & Manasian 1954, Halisky & Barbe 1962.

Fig. 49 A, B, C, E. Melanopsichium pennsylvanicum Hirschh. on Polygonum lapathifolium.

D. M. austro-americanum on P. punctatum, type.

- A. Sori in the inflorescence and on a leaf (arrow). Habit (HUV 1337; Bar = 1 cm).
- **B.** T.S. of a sorus (after Săvulescu & Manasian 1954:623).
- C. Spores in LM (HUV 1337; Bar = $10 \mu m$).
- **D.** Spores in SEM (LPS 3136; Bar = $10 \mu m$).
- E. Spore germination (after Săvulescu & Manasian 1954:628).



50. MELANOTAENIUM A. de Bary, s. str.

Bot. Zeitung (Berlin) 32:105, 1874.

ENTYLOMA de Bary subgen. MELANOTAENIUM (de Bary) Ciferri, Quad. Lab. Crittog. Ist. Bot. Univ. Pavia 27:171, 1963b. — Typus subgeneris: Melanotaenium endogenum (Unger) de Bary.

Sori in leaves, stems or roots of dicotyledonous host plants as black or dark lead-colored spots or swellings. *Spores* embedded in the host tissue, single, often aggregated, not powdery, dark-colored (reddish brown), thick-walled. *Spore germination* of *Tilletia*-type. *Host-parasite interaction* by haustoria. *Septal pore* simple, with membrane caps, inner membranous plates lacking.

Melanotaenium s. str., in the Melanotaeniaceae, has 9 known species parasitizing dicotyledonous host plants in various families. Ultrastructure, molecular analyses and germination types showed that Melanotaenium and dark-spored Entyloma species of monocotyledonous host plants (Cyperaceae, Poaceae and others) do not belong to these genera but to Jamesdicksonia, Phragmotaenium or Eballistra depending on spore germination (comp. these genera and also Bauer, Begerow, Nagler & Oberwinkler, 2001). Type of the genus:

Melanotaenium endogenum (F. Unger) H.A. de Bary,

Bot. Zeitung (Berlin) 32:106, 1874.

Protomyces endogenus Unger, Die Exantheme der Pflanzen, etc.:342, 1833. — Physoderma endogenum (Unger) Cornu, Ann. Sci. Nat. Bot., Sér. 6, 15:291, 1883. — Type on Galium mollugo, Austria, Tirol, Kitzbühel, leg. F. Unger.

Protomyces galii T. Nees & Henry, Das System der Pilze, Abth. 1:10, 1837 (nom. nov. superfl. pro P. endogenus).

Sori (Fig. 50 A) in stems and leaves as grayish black, minute pustules, scattered, in rows or often on the whole surface of the stems and on the base of the median vein of the leaves, covered by the epidermis. Host plants more or less deformed, often stunted, branched, with small leaves or, alternatively, with elongate internodes and almost normal leaves. Infected plants do not flower. Spore mass black, agglutinated, not powdery. Spores (Figs. 50 B, C) subglobose, ovoid, mostly irregular, 13-21.5 x 17-24 µm, dark reddish brown; wall smooth, two-layered, unequally 1-3 µm thick. Spore germination (Fig. 50 D): On the tip of a broad, aseptate basidium 2-9 finger-like basidiospores develop from which, without or after fusion of two spores, branched hyphae arise. From the hyphae, or occasionally directly from the basidiospores, typical ballistospores are produced on aerial sterigmata. Ballistospores germinate either by hyphae or by repetition (Woronin 1882('1881'):583, Pl. IV, figs. 30-35, Ingold 1988b:713, fig. 1).

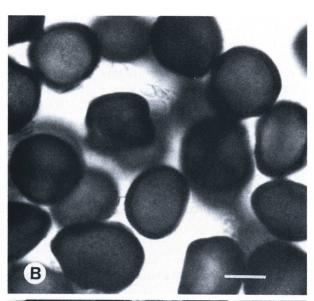
On Rubiaceae: Asperula hirsuta Desf., Galium biebersteinii Ehrend., G. boreale L., G. mollugo L., G. odoratum (L.) Scop. (Asperula odorata L.), G. verum L.; Europe, N Africa, Asia.

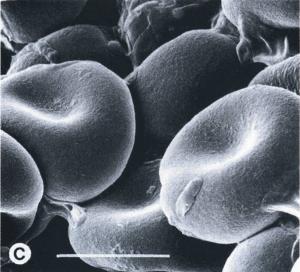
Ref.: Woronin 1882('1881'), Magnus 1892, Beer 1920, Liro 1938, Srinivasan & Thirumalachar 1964('1963'), Zambettakis & Joly 1972, Ingold 1988b, Negrean & Constantinescu 1997, Bauer, Begerow, Nagler & Oberwinkler 2001.

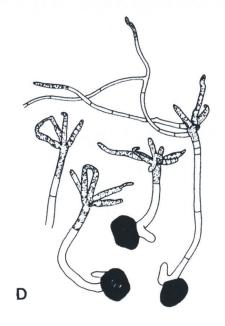
Fig. 50 A-C. Melanotaenium endogenum on Galium mollugo, Vánky, Ust. exs. no. 610, HUV 13239.

- **A.** Sori on stems and leaves. Habit (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$).
- D. Spore germination (after Woronin 1882('1881'), Pl. IV).









51. *MELANOXA* M. Lutz, K. Vánky & R. Bauer, *Mycol. Progr. 11*:155, 2012.

Sori on vegetative parts of host plants in Oxalidaceae, lead-colored, with agglutinated spore masses embedded in the host tissues, not powdery. *Spores* single, not forming balls, pigmented (yellowish brown, no violet tint), spore wall in TEM multilayered. *Host-parasite interaction* by haustoria. *Septal pore* simple, enclosed by membrane caps.

Melanoxa, in the Urocystidaceae, has two known species: **1.** *M. oxalidiellae* M. Lutz, Vánky & R. Bauer, on *Oxalis acetosella*, Slovenia, and **2.** The *type of the genus*:

Melanoxa oxalidis (S.M. Dietz & G.W. Fischer) M. Lutz, K. Vánky & R. Bauer, Mycol. Progr. 11:157, 2012.

Melanotaenium oxalidis Dietz & G.W. Fischer, Mycologia 62:405, 1970. — Type on Oxalis oregana, USA, Washington, Jefferson Co, upper Quinault River, date unknown, leg. S.M. Sherl & G.W. Fischer, WSP 58114. Paratype: Washington, Olympic Peninsula, Olympic National Forest, 22.VII.1956, leg. G.W. Fischer, WSP 45142; isoparatype HUV 1436!

Sori (Fig. 51 A) on the petioles and midribs of the leaves, swollen, lead-colored. Diseased parts often hypertrophied and contorted. Spore mass agglutinated, embedded in the host tissue, covered by the epidermis. Spores (Figs. 51 B, C) subpolyhedrally irregular, usually elongate, often with one or two subacute or acute tips, more rarely globoid or ellipsoidal, $10.5-17.5 \times 14-26.5(-28)$ µm, clear yellowish brown; wall 2-5(-7) µm thick, smooth.

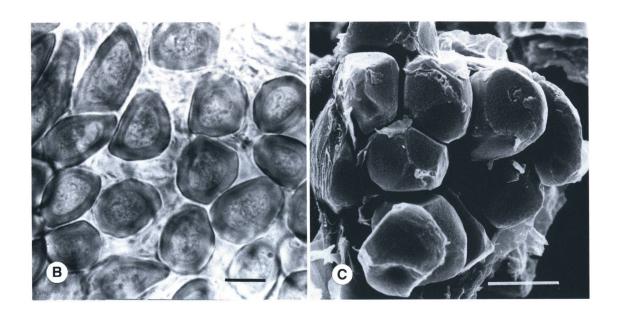
On Oxalidaceae: Oxalis oregana Nutt.; N America (USA).

Ref.: Lutz, Vánky & Bauer 2012, Vánky 2011('2012').

Fig. 51 A-C. Melanoxa oxalidis on Oxalis oregana, isoparatype, HUV 1436.

- A. Sori on the petiole and midribs of a leaf (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$).





52. MELANUSTILOSPORA C. Denchev,

Mycotaxon 87:476, 2003.

Sori on leaves of plants in Araceae, as dark, blackish gray, not powdery, pustular spots. *Spores* embedded in the host tissues, single, pigmented (blackish brown), thick-walled. *Host-parasite interaction* by haustoria. *Septal pore* simple, with membrane caps and two non-membranous plates closing the pore.

Melanustilospora, in the Urocystidaceae, has two known species: **1.** *M. arisari* (Peglion) Denchev, on *Arisarum proboscideum*, Italy, and **2.** The *type of the genus*:

Melanustilospora ari (M.C. Cooke) C. Denchev,

Mycotaxon 87:476, 2003.

Protomyces ari Cooke, Grevillea 1:7, 1872. — Melanotaenium ari (Cooke) Lagerheim, Bull. Soc. Mycol. France 15:98, 1899. — Type on Arum maculatum, England, Chichester, V.1872, leg. F.V. Paxton.

Ustilago plumbea Rostrup, in Thümen, Mycoth. univ. no. 531, 1876. — Melanotaenium plumbeum (Rostr.) Pirotta, Nuovo Giorn. Bot. Ital. 21:312, 1889 (as 'Melanothaenium'). — Type on Arum maculatum, Denmark, Funen, Tiselholt, VI.1875, leg. E. Rostrup, HUV 9094!; isotypes in Thümen, Mycoth. univ. no. 531, HUV 1382! Sori (Fig. 52 A) in leaves and petioles as lead-colored pustules with irregular, distinct margins, often clustered or in rows, covered by the epidermis. Spores (Figs. 52 B, C) globose, ovoid, mostly irregular, angular,

clustered or in rows, covered by the epidermis. *Spores* (Figs. 52 B, C) globose, ovoid, mostly irregular, angular, $12\text{-}15 \times 12\text{-}20 \,\mu\text{m}$, yellowish brown to dark olivaceous brown; wall 2-5 μ m thick, two-layered, endospore evenly c. 1.5 μ m thick, exospore light-colored, unevenly 0.5-3.5 μ m thick, often pierced by one to several narrow, thin-walled protuberances of the endospore (germ pores?).

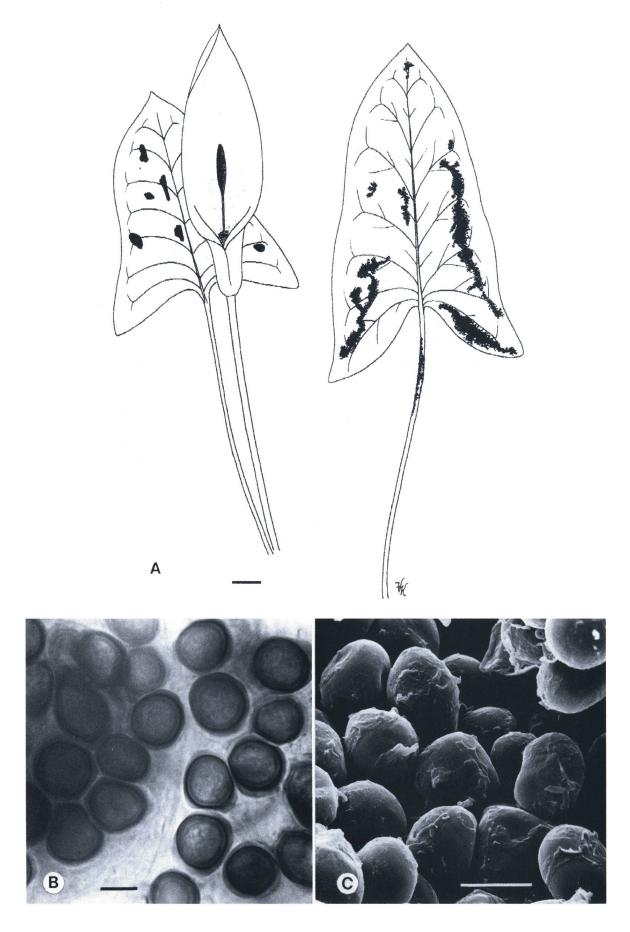
On Araceae: Arum cylindraceum Gasp., A. elongatum Steven, A. italicum Miller, A. maculatum L., A. orientale Bieb. (incl. A. besseranum Schott), Biarum tenuifolium (L.) Schott; Europe.

Ref.: Denchey 2003.

Fig. 52 A-C. *Melanustilospora ari* on *Arum maculatum*, Vánky, Ust. exs. no. 226 (as *Melanotaenium ari*), HUV 6826.

A. Sori on a leaf. Flower and a naturally pigmented leaf (left).

B, C. Spores in LM and in SEM.



53. MICROBOTRYUM J.H. Léveillé, s. lat.,

Ann. Sci. Nat. Bot., Sér. 3, 8:372, 1847; emend. Vánky, Mycotaxon 67:39, 1998.

BAUHINUS R.T. Moore, Mycotaxon 45:98, 1992. — Type: B. tragopogonis-pratensis (Pers.) R.T. Moore. (Syn. by Vánky, 1993:41).

HARADAEA Denchev, in Denchev, Moore & Shin, *Mycol. Balcan. 3*:72, 2006. Type: *H. duriaeana* (Tul. & C. Tul.) Denchev & H.D. Shin. (Syn. by Vánky 2011('2012'):344).

Sori in various organs of the host plants in dicotyledonous families. Spore mass dusty, pale to dark purplish brown. Spores solitary, pale to dark violet-brown; surface variously ornamented (often reticulate, also echinulate, verrucose or striate). Peridium, columella and capillitium-like threads absent in the sori. Sterile cells absent between the spores that are not catenulate. Spore germination results in phragmobasidia with successive production of sessile basidiospores, sterigmata absent. Host-parasite interaction by intercellular hyphae lacking interactions with deposits of specific fungal vesicles. Mature septa poreless.

The genus *Microbotryum* was reinstated by Deml & Oberwinkler (1982) for seven anthericolous smut fungi of the Caryophyllaceae family. It was studied and widened by Deml & Prillinger (in Prillinger *et al.* 1991), by Bauer *et al.* (1997), and revised by Vánky (1998c). It belongs to the Microbotryaceae in the Microbotryales of the Urediniomycetes. Ninety-four species of *Microbotryum* are recognized, parasitizing dicotyledonous plants belonging to ten families. *Type of the genus: M. antherarum* [DC.] Lév. (= *M. violaceum*):

Microbotryum violaceum (C.H. Persoon : C.H. Persoon) G. Deml & F. Oberwinkler, *Phytopathol. Z. 104*:353, 1982.

Uredo violacea Persoon, *Tent. Disp. fung.*:57, 1797. — Neotype on *Silene nutans*, (design. by Lutz *et al.* 2008:1292) Germany, Saxony-Anhalt, Gniest, 19.VI.1998, leg. H. Jage, GLM 50283 (For comments on the type see also Nannfeldt, in Lindeberg 1959:142).

For nomenclatural and taxonomic synonyms of *M. violaceum*, such as *Uredo violacea* Pers.: Pers., *Ustilago violacea* (Pers.: Pers.) Roussel, *Ust. violacea* (Pers.: Pers.) Fuckel, or *Uredo antherarum* DC., *Uredo antherarum* DC. α *silenes-nutantis* DC., *Ust. coronariae* Liro, see Vánky, *Illustrated genera* 2nd ed., 2002:100.

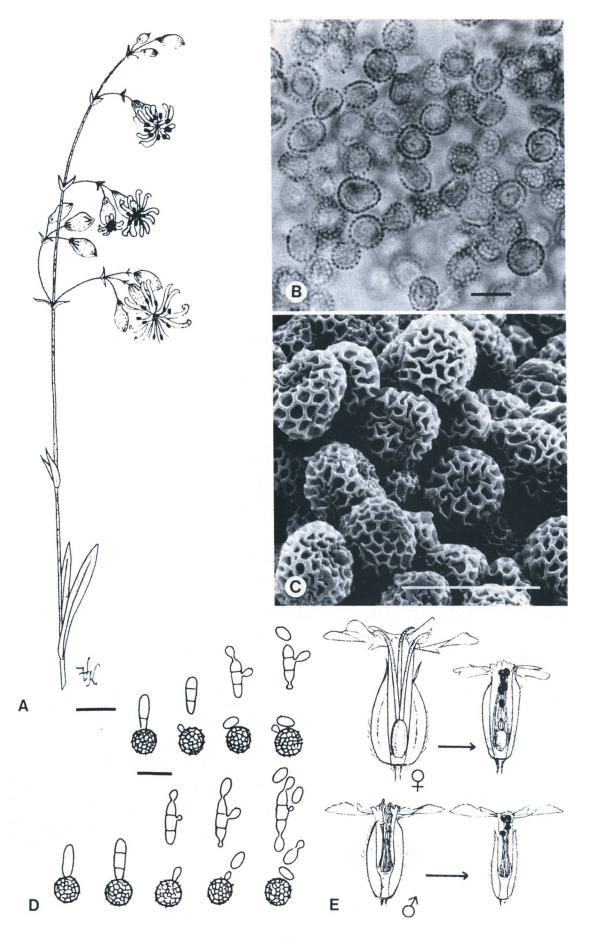
Sori (Fig. 53 A) in swollen anthers. Spore mass brownish violet, powdery. Spores (Figs. 53 B, C) globose to slightly ellipsoidal, (5-)6-8(-9) × (5-)6-9 μm, pale violet; wall reticulate, 5-7 meshes per spore diam., meshes rounded to regularly polygonal, up to 1 μm in diameter, muri 0.15-0.35 μm high, somewhat unevenly high, in median view with rounded edges, in SEM interspaces smooth. Spore germination (Fig. 53 D) results in 4-celled basidia (in 3 + 1 arrangement, where one cell usually remains included in the spore). On the basidia, laterally and terminally, ovoid, sessile basidiospores are produced. The basidial cells separate easily and continue to produce basidiospores or, in nutrient media, yeast cultures (Brefeld 1883:36, Pl. I, figs. 1-27, Deml & Oberwinkler 1982:384, Ingold 1983:577, fig. 5). Infection may occur in seedling stage and become systemic, or take place through the stigma, by spores transferred by pollinating insects, leading to semi-systemic infection (Baker 1947). When the pistillate plants of the dioecious Silene alba L. are infected (Fig. 53 E), the staminal rudiments develop into stamens containing smut spores instead of pollen and the ovules are reduced and become sterile (Werth 1911).

On Caryophyllaceae (subfam. Silenoideae): *Gypsophila, Lychnis* (incl. *Coronaria* and *Viscaria*), *Saponaria*, *Silene* species, world-wide.

Ref.: Werth 1911, Zillig 1921, Goldschmidt 1928, Nannfeldt in Lindeberg 1959, Day & Jones 1969, Deml & Oberwinkler 1982, Ingold 1983, Prillinger *et al.* 1991, Bauer, Oberwinkler & Vánky 1997, Begerow, Bauer, Oberwinkler 1998('1997'), Vánky 1998a, 1998c, Swann, Frieders & McLaughlin 1999, Vánky 2004a.

Fig. 53 A-C. *Microbotryum violaceum* on *Silene nutans* L., Thümen, Mycoth. univ. no. 23, HUV 5094. **D-E.** *M. violaceum* on *Silene alba* (Miller) E.H.L. Krause.

A. Sori in the anthers. Habit (Bar = 1 cm). **B, C.** Spores in LM and in SEM (Bars = 10 μ m). **D.** Spore germination (on MA, at room temp., in 1 day; after Ingold 1983:579). **E.** "Transvestitism" produced by *M. violaceum* infecting female flowers of the dioecious *Silene alba*, transforming them into male flowers (after Werth 1911:428).



54. MOESZIOMYCES K. Vánky,

Bot. Not. 130:133, 1977, emend. Vánky, Nord. J. Bot. 6:68, 1986.

TOLYPOSPORIDIUM Thirumalachar & Neergaard, Friesia 11:179, 25.II.1978('1977'). — Type: T. evernium (H. Sydow) Thirum. & Neerg. (= Moesziomyces bullatus) on Paspalum distichum. (Syn. by Vánky 1985a:89). TOLYPODERMA Thirum. & O'Brien, in Thirumalachar & Neergaard, Friesia 11:190, 25.II.1978('1977'), nom. nud. (Syn. by Vánky 1985a:89).

Sori in ovaries of host plants in Poaceae, without a columella. Spores in many-spored balls, firmly agglutinated and mixed with sterile cells, no cortex of sterile cells. Sterile cells thin-walled, rupturing when the spores are separated and appearing as irregular meshes or wings attached to the spore surface. Spore germination of Ustilago-type. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Moesziomyces was revised by Vánky (1986, 2005b). It belongs to the Ustilaginaceae. Currently it has only one species, the *type of the genus*:

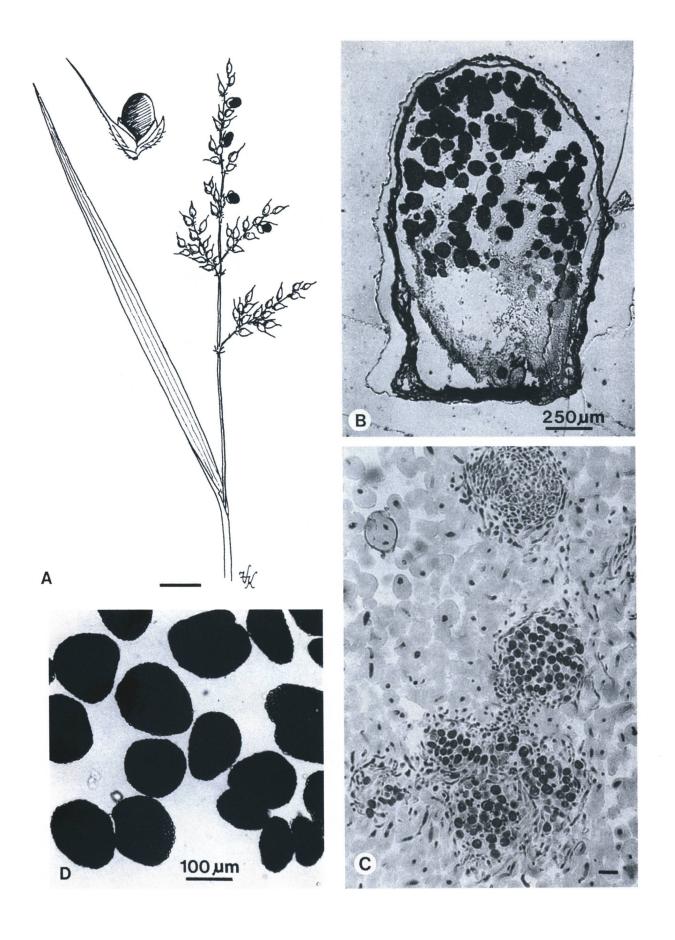
Moesziomyces bullatus (J. Schröter) K. Vánky,

Bot. Not. 130:133, 1977.

Sorosporium bullatum J. Schröter, Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss. 1869/72:6, 1869 (as "Sorisporium"). — Tolyposporium bullatum (J. Schröter) J. Schröter, in Cohn, Krypt. Fl. Schles. 3:276, 1887. — Tolypoderma bullata (J. Schröter) Thirum. & O'Brien, in Thirumalachar & Neergaard, Friesia 11:190, 1978('1977'), (as "bullatum"), invalid name, Tolypoderma being a nomen nudum (Art. 43.1 of the ICBN). — Lectotype (design. by Vánky 1977:133) on Panicum crus-galli (= Echinochloa crus-galli), Germany, Silesia, near Liegnitz [= Poland, Legnica], IX.1869, leg. G.W. Schneider, HUV 2442!; isolectotypes in Rbh., Fgi. eur. no. 1489.

For taxonomic synonyms as *Thecaphora globuligera* Berk. & Broome, and *Testicularia leersiae* Cornu, both on *Leersia hexandra, Tolyposporium penicillariae* Bref. on *Penicillaria spicata* (= *Pennisetum glaucum*), *Tolyposporium minus* J. Schröter on *Panicum* sp. (= *Echinochloa* sp.), *Ustilago verrucosa* J. Schröter on *Paspalum distichum*, *Tolyposporium senegalense* Speg. on *Penicillaria typhoidea, Tolyposporium evernium* H. Sydow on *Paspalum distichum*, and *Tolyposporium paspali* Langdon on *Paspalum distichum*, see Illustrated genera of smut fungi 2nd ed. (Vánky 2002:102).

Sori (Figs. 54 A, B) in ovaries, scattered in the inflorescence, globose to ovoid, 2-4(-5) mm long, covered by a smooth, initially green, later brown peridium of host tissue. Infection floral, through the stigma and style, possible only before the pollination of the flowers (Bhatt 1946). The entire sorus may fall off the plant or first the peridium ruptures irregularly exposing a granular, dark brown mass of spore balls; columella absent. Hyphae intracellular (Luttrell 1987:2585, figs. 12-15). Spore balls (Figs. 54 C, D, E) varying in shape and size, globose, subglobose, ovoid, elongate to irregular, (35-)50-240 x (40-)60-320 μm, dark brown, opaque, composed of numerous, up to several hundred spores united by sterile fungal cells, no cortex of sterile cells. Spores (Figs. 54 E, F, G, H, I) globose, ovoid to irregular, slightly polyhedral, subhyaline to pale yellowish brown, 6.5-9(-10) x 7-12(-13) μm, usually with several, more or less well-developed extensions (spore processes) and also remnants of the broken walls of the sterile cells; wall 0.5-0.7 μm thick, smooth. The spores are separated by sterile cells but in several places they remain in contact with each other by protuberances (Fig. 54 F). Sterile cells (Figs. 54 F, H, I) empty at maturity, thin-walled (0.1-0.2 μm, measured in TEM), appearing as irregular meshes or wings on the spore surface when the spores are separated. Spore germination (Fig. 54 J) results in septate basidia producing basidiospores laterally and terminally, on well-developed sterigmata (see also Setchell 1894:189, Pl. XVIII, figs. 2-4, Brefeld 1895:152, Pl. IX, figs. 25-40, Ingold 1988a:513, fig. 7).



On Poaceae: Echinochloa crus-galli (L.) P. Beauv. (Panicum crus-galli L.), E. frumentacea Link (E. crus-galli var. frumentacea (Link) E.G. Camus & A. Camus; E. crus-galli var. edulis Hitchc.), E. pungens (Poir.) Rydb. (E. muricata (P. Beauv.) Fernald), E. walteri (Pursh) A. Heller, Leersia hexandra Sw. (Homalocenchrus hexandrus Kuntze), L. japonica Makino, Leersia sp., Panicum hirticaule J. Presl, Paspalum distichum L., Pennisetum glaucum (L.) R.Br. (Penn. americanum (L.) Leeke; Penn. typhoides (Burm. fil.) Stapf & C.E. Hubb.; Penicillaria spicata (L.) Willd.), Penn. purpureum Schumach., Polytrias indica (Houtt.) Veldkamp (Po. amaura (Büse) Kuntze), Uranthoecium truncatum (Maiden & Betche) Stapf; cosmopolitan.

Moesziomyces bullatus is often mistaken for the floral sori of Ustilago trichophora (Link) Körnicke. However, an excellent distinguishing character is the sorus membrane, thin and smooth in M. bullatus, thick and hispid in U. trichophora.

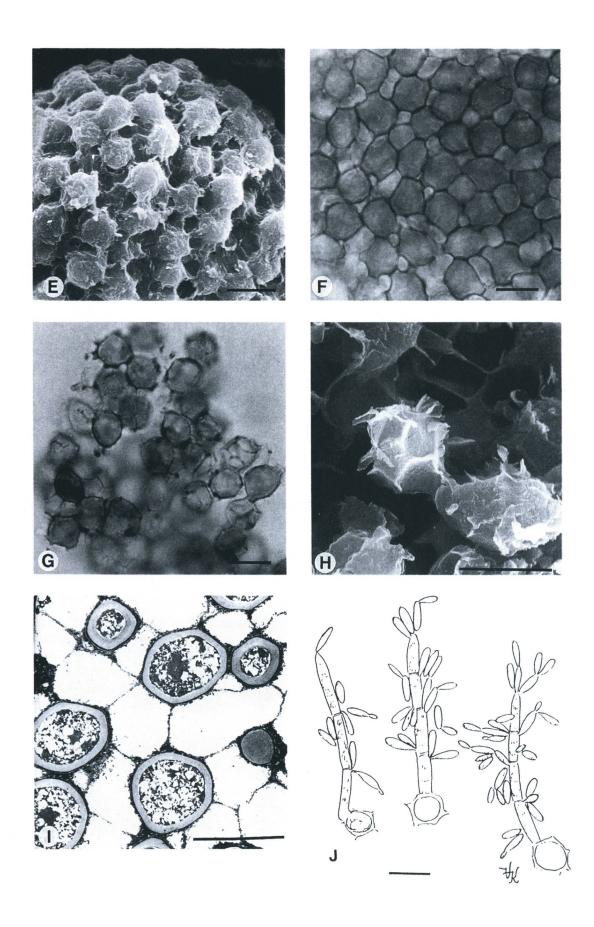
In early spore ball formation, young sori are completely filled by a network of sporogenous hyphae, in which spore ball initials appear as small concentrations of protoplasm rich cells (Fig. 54 C). With age these cells become wider, and loosely situated spore-initials are differentiated. These increase in size but are separated from each other by colorless, swollen cells, which later are transformed into sterile cells. In this stage, spore balls of all ages can be seen in the same sorus: mature ones especially in the distal part, the basal part still filled by sporogenous hyphae and young spore balls. Finally, all sporogenous hyphae are transformed into spore balls and the sorus is filled with mature spore balls (Vánky 1985a:91).

The basidium is two- to four-celled in the smut on *Echinochloa crus-galli* (Brefeld 1895:152, Ingold 1988a:513) but four-celled on *Pennisetum glaucum* (L.) R.Br. (*P. typhoideum* L.; *P. americanum* Schumacher; *Penicillaria spicata* Willd.; Brefeld 1895:154, Pl. IX, figs. 35-40, Yen 1938:88, Viswanathan 1959, Subba Rao & Thakur 1983). This difference may depend on different external conditions during germination, but could also be genetically determined. If the difference is constant and genetic, in spite of the morphological similarities of the spore balls and spores, *Moesziomyces bullatus* and *M. penicillariae* should be treated as different taxa.

Spores from pearl millet (*Pennisetum glaucum* (L.) R.Br.) germinated without resting period (Ajrekar 1931, Subba Rao & Thakur 1983), or next year (Yen 1938) showing the same characters as those from *Echinochloa*.

Ref.: Setchell 1894, Brefeld 1895, Ajrekar 1931, Bhatt 1946, Viswanathan 1959, Vánky 1977, 1986, 2005b, Thirumalachar & Neergaard 1978('1977'), Subba Rao & Thakur 1983.

- Fig. 54 A-J. Moesziomyces bullatus. A, B, C, E, G, H. on Echinochloa crus-galli, Vánky, Ust. exs. no. 35 (as Tolyposporium bullatum), HUV 2456. F. on Leersia japonica, HUV 5218, and D, J. on Paspalum distichum, Vánky, Ust. exs. no. 833, HUV 15725.
- A. Sori in some ovaries in the inflorescence. Habit (Bar = 1 cm), and an enlarged sorus.
- **B.** L.S. of a young sorus with spore balls in formation.
- C. Young spore balls in different stages of their development (T.S., stained; Bar = $10 \mu m$).
- **D**, **E**. Spore balls in LM and in SEM.
- **F, G, H, I.** Spores and sterile cells in LM, in SEM and in TEM (Bars = $10 \mu m$).
- **J.** Spore germination (on WA, at room temp., in 3 days; Bar = $10 \mu m$).



55. MOREAUA T.N. Liou & H.C. Cheng,

Contr. Inst. Bot. Natl. Acad. Peiping, 6:209, 1949; emend. Vánky, Mycotaxon 74:351, 2000.

Sori naked on the surface of inner floral organs of plants in Cyperaceae, composed of a black, granular-powdery mass of spore balls. Columella, peridium and sterile cells lacking. Spore balls composed of rather firmly cohering spores. Spores usually wedge-shaped, pigmented (reddish- or blackish brown), wall thick on the free surface. Spore germination results in four-celled phragmobasidia with sessile basidiospores. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Moreaua, in the Anthracoideaceae, has 38 known species on host plants belonging to 15 genera of Cyperaceae, predominantly in the southern hemisphere. It was revised and emended by Vánky (2000b). *Type of the genus: Moreaua kungii* Liou & H.C. Cheng (= *M. aterrima*).

Moreaua aterrima (Tul. & C. Tul.) K. Vánky,

Mycotaxon 74:351, 2000.

Thecaphora aterrima Tul. & C. Tulasne, Ann. Sci. Nat. Bot., Sér. 3, 7:110, 1847. — Tolyposporium aterrimum (Tul. & C. Tul.) Dietel, in Engler & Prantl, Die Natürl. Pflanzenfam. I:14, 1897. — Lectotype (design. by Liro 1938:310) on Carex praecox Jacq. (= C. caryophyllea), France, Vienne Dépt., Pictavia [= Poitiers], leg. S. Delacroix.

Sorosporium atrum Peck, Bot. Gaz. (Crawfordsville) 5:35, 1880. — Type on Carex pennsylvanica, USA, Colorado, alt. c. 1800 m, VI, leg. M.E. Jones. (Syn. by Clinton 1902:129).

Sorosporium flahaultii Boyer & Jaczewski, Bull. Soc. Bot. France 40:CCLXXVII, 1894. — Type on Carex olbiensis, France, Hérault Dépt., "Bois de Montarnaud" near Montpellier, leg. Ch. Flahault.

Sorosporium caricis Ferraris, Annario Reale Ist. Bot. Roma 9:191, 1902. — Type on Carex praecox, Italy, Piemonte, Pinerolo, V.1861, leg. A. Carestia.

Moreaua kungii Liou & H.C. Cheng, Contr. Inst. Bot. Natl. Acad. Peiping, 6:209, 1949. — Type on Carex sp., China, Shensi [= Shaanxi] Prov., Chow-chih-hsien, Low-kwan-tai, on river bank, 22.IV.1938, leg. H.W. Kung 55; isotype HUV 11698!

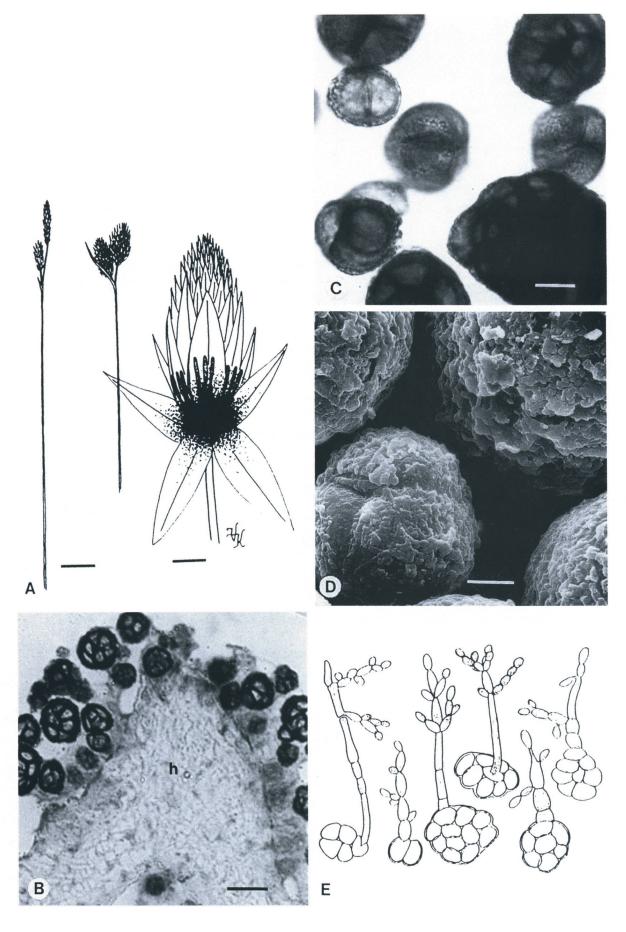
Sori (Figs. 55 A, B) on filaments and the base of bracts of staminate flowers, only exceptionally on more or less aborted perigynia, as a black, granular-powdery mass of spore balls concealed by the bracts. Infection systemic. Infected female flowers more or less completely transformed into male flowers with sori. Spore balls (Figs. 55 B, C, D) globose, ovoid to irregular, 16-45 μm long, yellowish brown to blackish brown, persistent, composed of (1-)2-15 (or more?) spores. Spores (Figs. 55 C, D) subglobose, hemiglobose, subcuneiform, polyhedral to irregular, flattened and smooth on the contact sides, convex, thick-walled, finely and densely verruculose on the free surface, 7-14 x 10-16 μm, pale yellowish brown to dark olive-brown. Spore germination (Fig. 55 E) results in phragmobasidia on which ovoid basidiospores are produced laterally or often terminally. Basidiospores germinate giving rise to chains or groups of yeast-like cells. After conjugation of basidial cells, or of basidiospores, hyphae may result (Cocconi 1890:706, Pl. I(3), figs. 1-11, Liou & Cheng 1949, Pls. IV-VI).

On Cyperaceae: Carex adusta Boott, C. asturica Boiss., C. caryophyllea Latourr. (C. praecox Jacq., non Schreb.; C. verna Chaix, non Lam.), C. curvula All., C. depressa Link, C. ericetorum Pollich, C. filifolia Nutt., C. halleriana Asso, C. humilis Leysser, C. kirganica Kom., C. lanceolata Boott, C. michelii Host, C. montana L., C. olbiensis Jordan, C. pennsylvanica Lam., C. pilulifera L., C. praecox Schreber, C. pyrenaica Wahlenb., C. sempervirens Vill., C. tomentosa L., C. vanheurckii Muell. Arg.; Europe, Asia, N America.

Ref.: Cocconi 1890, Liou & Cheng 1949, Vánky 2000b.

Fig. 55 A-D. Moreaua aterrima on Carex caryophyllea, Vánky, Ust. exs. no. 6, HUV 2044.

- **A.** A healthy (left) and a diseased inflorescence (right). Habit (Bar = 1 cm). Enlarged a diseased spike with some opened spikelets showing the external sori on the filaments (Bar = 1.6 mm).
- **B.** Spore ball formation on the surface of a filament.
- C, D. Spore balls and spores in LM and in SEM (Bars = $10 \mu m$).
- E. Spore germination (after Liou & Cheng 1949).



56. MUNDKURELLA M.J. Thirumalachar,

Mycologia 36:594, 1944.

Sori in various organs of plants in Araliaceae, filled with spores mixed with sterile cells. Spores one- to several-celled, pigmented (brown), with rich cell contents. Sterile cells 1-celled, subhyaline to pale-colored, ornamented, usually collapsed. Spore germination results in phragmobasidia with lateral and terminal, sessile basidiospores. Host-parasite interaction by haustoria. Septal pore simple, with membrane caps and two non-membranous plates closing the pore.

Mundkurella is a member of the Urocystidaceae. It was treated by Vánky (1990b). Mundkurella has five known species: 1. M. japonica Denchev & Kakishima on Kalopanax form E Asia, 2. M. kalopanacis Vánky on Kalopanax form E Asia, 3. M. mossii Savile on Aralia from N America, 4. M. schefflerae Vánky, C. Vánky & McKenzie on Schefflera from New Zealand, and 5. The type of the genus:

Mundkurella heptapleuri M.J. Thirumalachar,

Mycologia 36:596, 1944.

Type on *Heptapleurum venulosum*, E India, Bangalore, Lal-Bagh, 15.VIII.1942, leg. M.J. Thirumalachar. Holotype HCIO 10133; isotypes BPI 192696, 192698, 192699, 192700, IMI, HUV 11506!

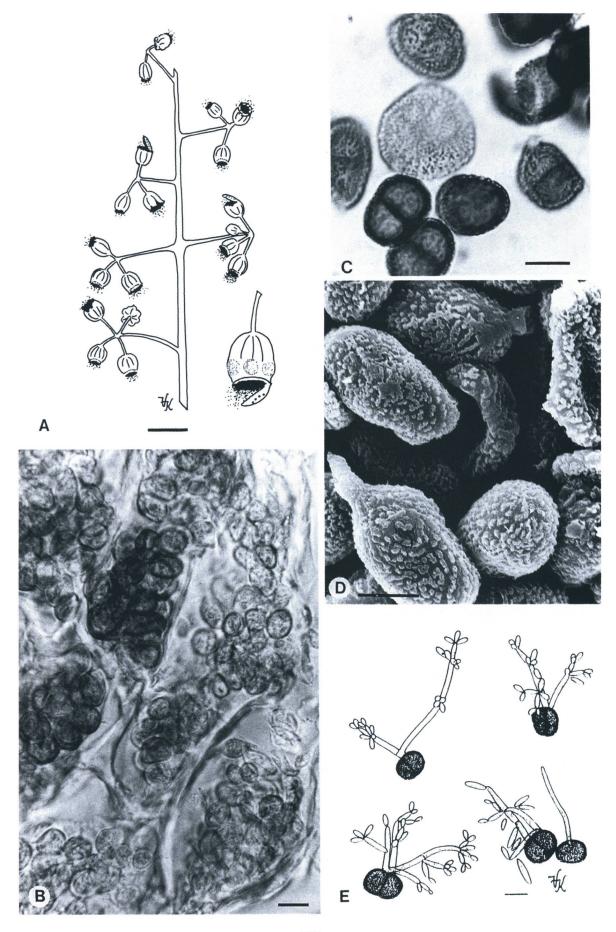
Sori (Figs. 56 A, B) in fruits, petioles, stems and leaves containing a black, semi-agglutinated to powdery mass of spores mixed with sterile cells. In fruits the endosperm and embryo are completely or rarely partially destroyed, only the testa remains intact holding the spores together; in stems the sori are subepidermal, completely replacing the meristematic tissues at the apex; in petioles and leaves the sori form black warts. Spores produced in large groups, on the end of sporogenous hyphae. Immature spores (Fig. 56 B) 1-celled, pale-colored. Spores (Figs. 56 C, D) when mature 1-2, rarely 3-4-celled, subglobose, ovoid, ellipsoidal to slightly irregular, 10-17 × 12-27 μm, deep chocolate-brown, contents granular; wall on the free surface 2-3 μm thick, including warts, composed of two layers, a dark brown, 0.5-1 μm thick inner layer, and a pale yellowish brown, 0.8-1.5(-2) μm thick, densely, rather coarsely verruculose outer layer, spore profile serrate. Warts c. 0.4-0.7 μm high, rounded or by confluence forming irregular groups or rows. Sterile cells unicellular, 13-24 × 16-30 μm, subglobose or ovoid, usually collapsed, pale yellow or hyaline; wall 1-2.5 μm thick, verruculose. Intermediate cells may occur. Spore germination (Fig. 56 E) results in septate basidia with basidiospores produced laterally and terminally.

On Araliaceae: *Heptapleurum venulosum* Seem.; S Asia (India). Known only from the type collection. Unfortunately, the host plant of the type specimen, an infected tree in the park of the botanical garden Lal-Bagh, was cut down (M.S. Patil, pers. comm.).

Ref.: Thirumalachar 1944, Savile 1975, Vánky 1990b, Vánky K., Vánky C. & McKenzie 1999.

Fig. 56 A-D. Mundkurella heptapleuri on Heptapleurum venulosum, isotype, HUV 11506.

- A. Sori in the fruits. Habit (Bar = 1 cm).
- **B.** T.S. of a sorus in LM, showing groups of spores in different stages of maturation (Bar = $10 \mu m$).
- C, D. Spores and sterile cells in LM and in SEM (Bars = $10 \mu m$).
- **E.** Germinating spores of *Mundkurella kalopanacis* Vánky on *Kalopanax pictus* (Thunb.) Nakai, Japan, Ibaraki Pref., Kukizaki-machi, 2.XI.1993, M. Kakishima, HUV 16732 (on WA, at room temp., in 2 days, R. Bauer; Bar = 10 μm).



57. MYCOSYRINX G. Beck,

Ann. K. K. Naturhist. Hofmus. (Wien) 9:123, 1894 (as "Mykosyrinx").

Sori forming strongly deformed, ramified witches' brooms on host plants in Vitaceae. Spores in pairs, dark-colored (brown), more or less hemispherical, connected on their flattened sides, initially embedded in the host tissue, later powdery. Spore germination of Mycosyrinx-type, i.e. the basidia are reduced to the spores, basidiospores sigmoid. Host-parasite interaction (Fig. 8, p. 24) by intercellular hyphae with enlarged interaction zones, no haustoria. Mature septa poreless.

Mycosyrinx belongs to the Mycosyringaceae, order Ustilaginales. It was treated by Vánky (1996b). It has four known species, all on Cissus species: 1. M. arabica (Henn.) Penzig from S Asia, 2. M. microspora Cant. from Africa and S America(?), 3. M. usambarensis (Henn.) Vánky from Africa, and 4. The type of the genus:

Mycosyrinx cissi (A.P. De Candolle) G. Beck, Ann. K. K. Naturhist. Hofmus. (Wien) 9:123, 1894.

Uredo cissi DC., in Poiret, Encycl. méth. Bot. 8:228, 1808 (as "cyssi"). — Ustilago? cissi (DC.) Tul. & C. Tulasne, Ann. Sci. Nat. Bot., Sér. 3, 7:92, 1847. — Schroeteria cissi (DC.) de Toni, in Saccardo, Syll. Fung. 7(2):501, 1888. — Geminella exotica J. Schröter var. decandollei A.A. Fischer v. Waldheim, Aperçu Syst. Ustil.:43, 1877 (nom. nov. illegit. pro Uredo cissi). — Type on Cissus sicyoides, Island of Saint Dominique (Dominican Rep.), leg. P.A. Poiteau.

Taxonomic synonyms are *Puccinia incarcerata* Lév., and *Geminella exotica* J. Schröter (comp. Vánky, *Smut Fungi of the World*, 2011('2012'):452).

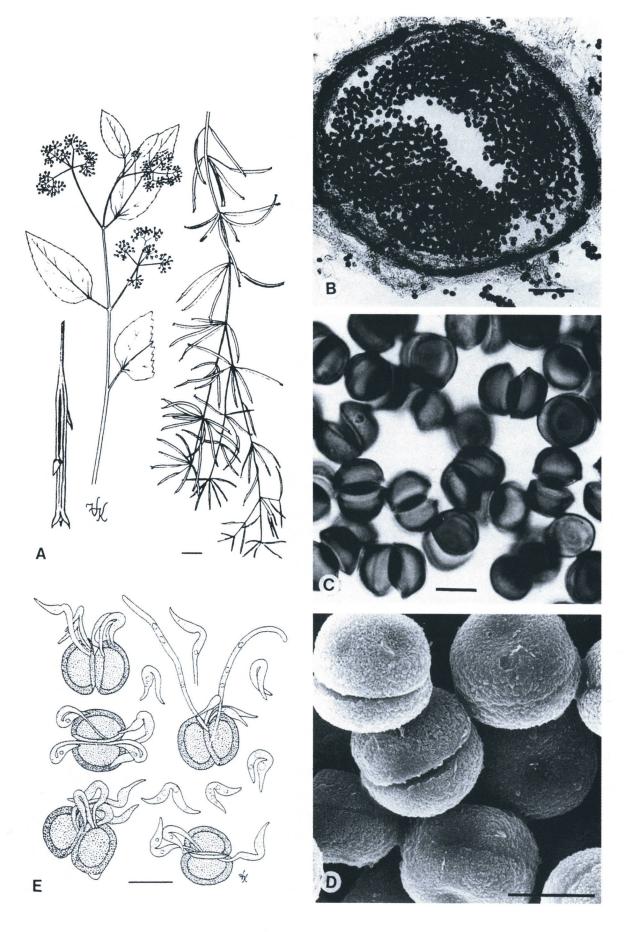
Sori (Figs. 57 A, B) in distal, cylindrical, swollen part of the branches, forming up to 1 m or longer, hanging, repeatedly branching witches' brooms. Single sori cylindrical, 1-2 x 5-30 mm, initially green, later brown, composed of an outer layer of host tissue and an inner, whitish layer of hyphae producing paired spores which fill the interior of the tubes. At maturity, the sori split longitudinally disclosing the black, powdery mass of spores. Spores (Figs. 57 C, D) in pairs arising from the division of the spore mother cell, connected in the middle of their flattened or, in rehydrated spores, slightly conical sides. Single spores in side view subhemicircular or subhemielliptic, 7-8.5(-9) μm wide, in plane view circular or elliptic, 9.5-12.5 x 10.5-13.5 μm, dark reddish brown; wall c. 1 μm thick, free surface minutely and densely punctate-verruculose, facing surface smooth. In LM, the two surfaces are delimited by a sharp, often slightly protruding line corresponding to a thin-walled germ ring. Spore germination (Fig. 57 E) results in up to four (rarely 5 or 6), peculiar and unique, bent basidiospores produced successively on very short, pedicel-like basidia or directly from the spores. Young basidiospores look like the neck and head of a swan. Mature basidiospores more or less strongly bent with an evidently swollen, asymmetrical part and two subacute ends, measuring 1.5-2.5 x 14-20 μm. Rarely, concomitantly with production of typical basidiospores, long hyphae may result from spore germination (comp. also Piepenbring & Bauer 1995:856, Vánky 1996b:177).

On Vitaceae: Cissus acida L., C. erosa Rich. (C. quadrialata H.B.K.), C. rhombifolia Vahl, C. sicyoides L., C. trifoliata L., Cissus sp.; N, C & S America, W Indies, Africa(?).

Ref.: Beck 1894, Penzig 1899, Iyengar & Narasimhan 1922, Cantournet 1948, Viennot-Bourgin 1952, Mordue 1988, Piepenbring & Bauer 1995, Piepenbring 1997('1995'), Vánky 1996b.

Fig. 57 A-E. *Mycosyrinx cissi* on *Cissus sicyoides*. A. Vánky, Ust. exs. no. 835, HUV 15727. B, C, D. USA, Florida, Fort Drum, 19.II.1950, D. Blake, HUV 1445. E. Costa Rica, Cartago Prov., near Monumento Nacional Guayabo, 2.I.1994, M. Piepenbring, HUV 16014.

A. Sori in swollen branches (floral pedicels?). A healthy inflorescence and a small part of a c. 1 m long witches' broom. Habit (Bar = 1 cm). Enlarged a ripe sorus. **B.** T.S. of a sorus, showing the external ring of host tissue (dark-colored), a thin layer of sporogenous hyphae (pale-colored), and the lumen filled with dark spore mass (Bar = $100 \mu m$). **C, D.** Spores in LM and in SEM (Bars = $10 \mu m$). **E.** Germinating spores (in WA, at 24-30 °C, in 4-7 days, R. Bauer; Bar = $10 \mu m$). Note the typical, strongly bent basidiospores (rarely also hyphae) produced on very short, pedicel-like basidia or directly from the spores.



58. NANNFELDTIOMYCES K. Vánky,

Sydowia 34:171, 1981.

Sori in leaves or stems of aquatic or paludal plants in Sparganiaceae, as inconspicuous spots. Spore balls embedded in the host tissue, extracellular, many-spored, friable and easily decomposing, lacking a cortical layer, formed of a network of thin, branched, modified hyphae in which the spores are scattered. Spores pale, loosely held together by the network of modified hyphae. Spore germination of Tilletia-type. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore is simple, with two membrane caps.

Nannfeldtiomyces belongs to the Doassansiaceae. Together with Burrillia, Doassansia, Entylomaster, Heterodoassansia, Narasimhania, Pseudodermatosorus, Pseudodoassansia, Pseudotracya and Tracya, they form a natural group both morphologically and ecologically (with complex spore balls on aquatic or paludal plants), and are phylogenetically related also with the single-spored Doassinga. Two species of Nannfeldtiomyces are known, both on Sparganium: 1. N. anomalus (Crowell) Vánky form Europe and N America, and 2. The type of the genus:

Nannfeldtiomyces sparganii (G. Lagerheim) K. Vánky, Sydowia 34:171, 1981.

Melanotaenium(?) sparganii Lagerheim, Bull. Soc. Mycol. France 15:98, 1899. — Entyloma sparganii (Lagerh.) Lagerh., in Palm, Svensk Bot. Tidskr. 4(1):(3), 1910. — Entyloma sparganii (Lagerh.) Ciferri, Atti Ist. Bot. Univ. Pavia, Ser. 3, 1:94, 1924 (comb. superfl.). — Neotype (design. by Vánky 1985a:92) on Sparganium ramosum (= S. erectum), Sweden, Drottningholm near Stockholm, IX.1910, leg. G. Lagerheim, HUV 7622!; isoneotypes in S and in Vgr., Micr. rar. sel. no. 1592, HUV 1265! Topotype: on 2.X.1975, leg. K. Vánky, UPS, HUV 2272!

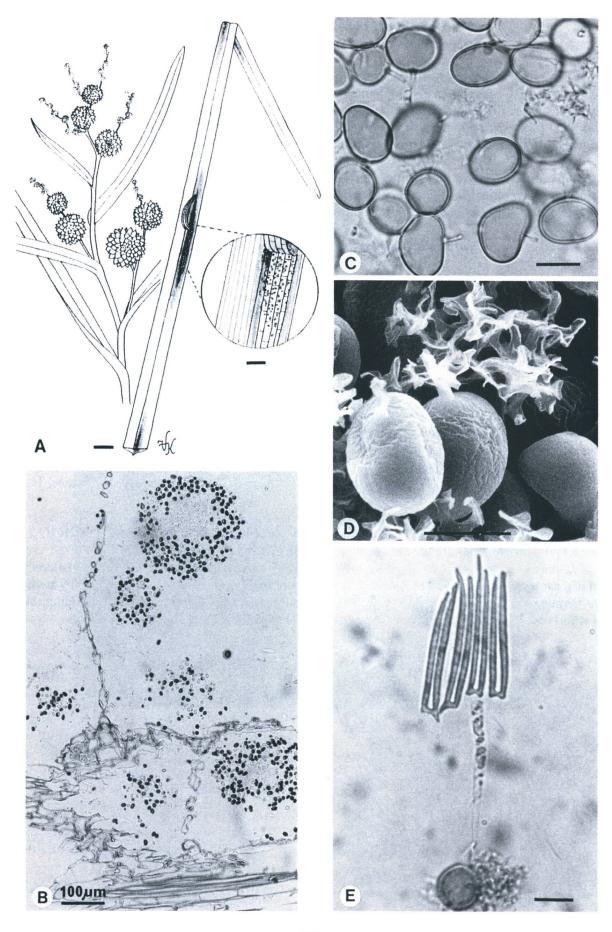
Burrillia acori Dearness, in Zundel, North American Flora 7:1026, 1939. — Type on Acorus calamus L. (= misnamed Sparganium eurycarpum Engelm., det. Savile 1957:279), Canada, Ont., 3 mile N of Puslinch Lake near Guelph, in a small lakelet, 2.VIII.1913, J. Dearness, DEARN 6306 in DAOM.

Sori (Figs. 58 A, B) in leaves as ovoid, fusiform or linear spots, from a few mm long to 0.5-1 x 5-15 cm, or more by fusion, initially inconspicuous, yellowish green, later pale yellowish brown, with indistinct margins. Spore balls (Figs. 58 A, B) in the leaf parenchyma, extracellularly in the lacunae, initially as white, agglomerated mycelia, resembling minute cotton balls, in which the spores are differentiated. Mature spore balls pale brown or beige, solitary or rarely confluent, globose to irregularly elongate, 100-500 μm long, composed of a network of branched, thin, modified hyphae (or the remains of hyphae) in which the spores are scattered. Spores often absent from the central part of the spore ball. Cortical layer (of spores, sterile cells or hyphae) lacking. Spores (Figs. 58 C, D) subglobose, ovoid, moderately elongate, slightly irregular, often indented on one side (bun-shaped), sometimes slightly curved (kidney-shaped), 9-11 x 10-16(-18) μm, pale yellowish brown; wall smooth, c. 0.5 μm thick and usually with two short mycelial appendages on opposite sides.

On Sparganiaceae: Sparganium erectum L. (S. ramosum Hudson), S. eurycarpum Engelm., Sparganium sp.; Europe, Asia, N America.

Ref.: Lagerheim 1899, Crowell 1942, Vánky 1981b.

- Fig. 58 A-D. Nannfeldtiomyces sparganii on Sparganium erectum, Vánky, Ust. exs. no. 350, HUV 10724.
- **A.** Sori in a leaf with spore balls embedded in the host tissue, evident when the epidermis is removed (see detail drawing; Bar = 3 mm).
- **B.** T.S. of a sorus with spore balls (stained; Bar = $100 \mu m$).
- C, D. Spores and fragments of the network of the branched, modified hyphae in LM and in SEM.
- **E.** Nannfeldtiomyces anomalus (Crowell) Vánky on Sparganium chlorocarpum Rydb., Vánky, Ust. exs. no. 349, and Fgi. exs. suec. no. 3001. A germinating spore (on WA, at room temp., in 1 day) with a holobasidium and 8, terminally developed, conjugated basidiospores (stained with cotton blue).



59. *NARASIMHANIA* M.J. Thirumalachar & M.S. Pavgi, *Sydowia* 6:390, 1952; emend. Vánky, *Sydowia* 34:174, 1981.

Sori in the leaves of plants in Alismataceae, forming pale spots with spore balls embedded in the host tissue. Spore balls permanent, often lobed and containing cavities clad by sterile cells. Spores in the ball scattered in a parenchymatous tissue of sterile fungal cells. A cortical layer of small sterile cells is present. Spore germination of Tilletia-type. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore is simple, with two membrane caps.

Narasimhania is currently a unispecific genus in the Doassansiaceae family. Morphologically, ecologically and phylogenetically allied with Burrillia, Doassansia, Entylomaster, Heterodoassansia, Nannfeldtiomyces, Pseudodermatosorus, Pseudodoassansia, Pseudotracya and Tracya. Type of the genus:

Narasimhania alismatis M.S. Pavgi & M.J. Thirumalachar, in Thirumalachar & Pavgi, *Sydowia* 6:390, 1952.

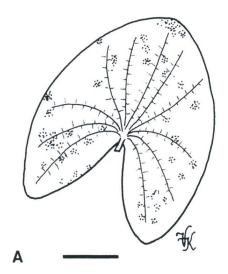
Type on "Alisma sp." (= Lophotocarpus guyanensis, det. K. Vánky), India, Uttar Pradesh, Banaras [= Varanasi], 12.IX.1951, leg. M.S. Pavgi, HCIO 20131; isotypes BPI 178876, IMI 52807, HUV 8637!

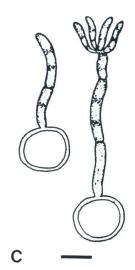
Sori (Fig. 59 A) in leaves forming pale yellow spots, 3-6 mm in diameter or larger by coalescence, with spore balls embedded in the host tissue, visible as minute, dark brown, punctate elevations. Spore balls (Fig. 59 B) permanent, subglobose to irregular, often lobed and appearing stellate, containing cavities clad by sterile cells. A rather indistinct cortical layer of sterile cells is present. Spores (Fig. 59 B) scattered in a parenchymatous tissue of sterile fungal cells, subglobose, subpolyhedral to slightly irregular, 6.5-9 x 7.5-15 μm, pale yellow; wall evenly c. 0.5 μm thick. Spore germination results in a basidium bearing a terminal whorl of 4-6 basidiospores (Thirumalachar & Pavgi 1952:391).

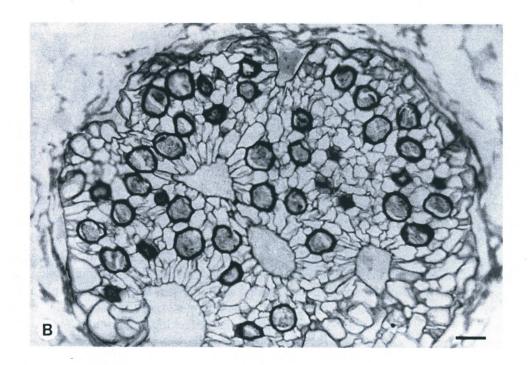
On Alismataceae: Lophotocarpus guyanensis (H. B. K.) J.G. Smith (Sagittaria guyanensis H. B. K.), Sagittaria montevidensis Cham. & Schlecht.; Africa (Mali), S Asia (India), S America (Brazil).

Ref.: Thirumalachar & Pavgi 1952, Singh & Pavgi 1977b, 1979, 1980, Vánky 1981b, Soares, Barreto & Braun 2009.

- Fig. 59 A-C. Narasimhania alismatis on Lophotocarpus guyanensis, isotype, HUV 8637 ex HCIO 20131.
- A. Sori on a leaf with spore balls embedded in the leaf tissue visible as minute dots.
- **B.** T.S. of a spore ball showing a rather indistinct cortical layer of sterile cells and the darker (colored) spores scattered in a parenchymatous tissue of fungal cells. The spore ball is lobed and has cavities clad by sterile cells.
- C. Spore germination (on slide, in moist chamber, at room temp., in 3 days) results in a basidium bearing a terminal whorl of 4-6 basidiospores (after Thirumalachar & Pavgi 1952, Pl. V, fig. 13).







60. *NEOVOSSIA* F. Körnicke,

Österr. Bot. Z. 29:217, 1879.

VOSSIA Thümen, Österr. Bot. Z. 29:19, 1879, later homonym, non Vossia Wallich & Griffith, 1836 (q.e. Poaceae), nec Vossia Adanson, 1763, nom. rej. (q.e. Aizoaceae).

Sori in ovaries of Poaceae, scattered in the inflorescence, filled with black, semi-dusty, not fetid spore mass. Spores large, dark-colored, foveolate, produced singly on the swollen ends of branched fertile hyphae, provided with a hyaline sheath tapering into a long, hyaline appendage, the remains of the sporogenous hypha. Spore germination results in holobasidia with numerous, terminally clustered basidiospores which do not fuse. Sterile cells absent. Host-parasite interaction by intercellular hyphae; interaction apparatus is lacking. Septal pore is a dolipore traversed by two membranous plates, pore caps lacking.

Neovossia currently considered to be a unispecific genus in the Tilletiaceae. It is related to *Tilletia*, *Conidiosporomyces*, *Ingoldiomyces* and *Oberwinkleria*. Typical for the type species, *N. moliniae*, are: the local infection, the elongate, finely foveolate spores possessing a long, hyaline appendage, the very large number of basidiospores which germinate without conjugation, the absence of the trimethylamine smell and the lack of sterile cells between the spores. *Type of the genus:*

Neovossia moliniae (F. Thümen) F. Körnicke,

Österr. Bot. Z. 29:217, 1879.

Vossia moliniae Thümen, in Thümen, Mycoth. univ. no. 1216, 1879; Österr. Bot. Z. 29:19, 1879. — Tilletia moliniae (Thümen) G. Winter, in Rabenh. Krypt.-Fl., 2 Aufl., 1(1):109, 1881. — Type on Molinia caerulea, Slovenia, Ljubljana [formerly Austria, Krain (Carniolia), Laibach], X.1878, leg. W. Voss, HUV 9092!; isotypes in Thümen, Mycoth. univ. no. 1216, HUV 1452!

Neovossia iowensis Hume & Hodson, in Hodson, Bot. Gaz. (Crawfordsville) 30:274, 1900. — Type on Phragmites communis (= Ph. australis), USA, Iowa, Colo, 23.IX.1899, leg. E.R. Hodson, BPI 174243; isotypes BPI 174244, 174250. (Syn. by Vánky 1990a:476).

Neovossia danubialis Săvulescu, Comun. Acad. Republ. Populare Române 5:63, 1955. — Type on Phragmites communis (= Ph. australis), Romania, Constanța Reg., Danube Delta, 8.X.1954, leg. E. Stănescu, BUCM; isotypes in Herb. myc. rom. no. 1636, HUV 1457! (Syn. by Vánky 1990a:476).

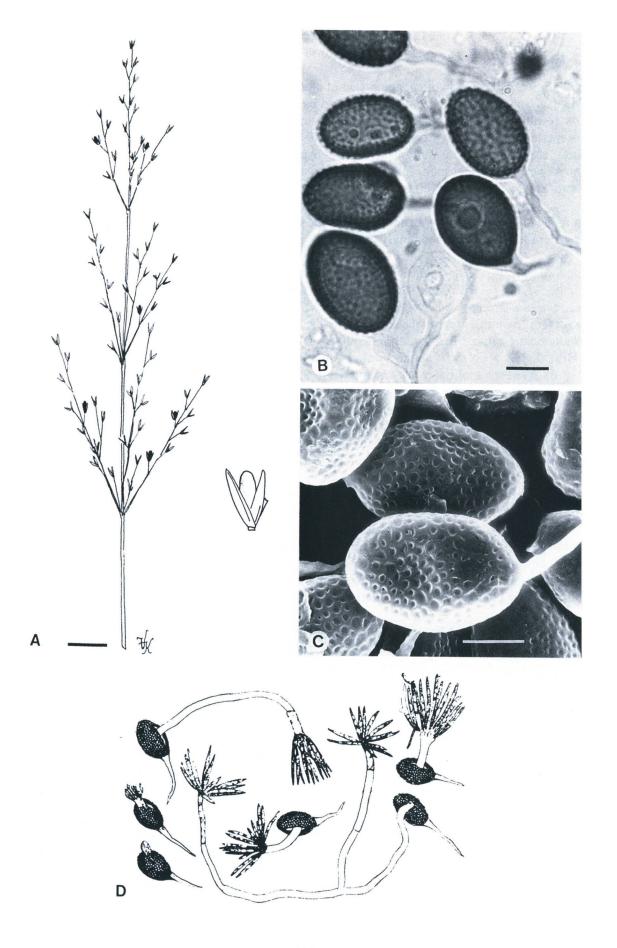
Sori (Fig. 60 A) in some ovaries of an inflorescence, rather inconspicuous, ovoid, ovoid-fusiform, sometimes slightly curved, 2-4(-5) mm long, appearing between the spreading lemma and palea, covered by the pericarp and an inner layer of sporogenous hyphae, initially green, later pale brown, usually detaching entirely or breaking to reveal the black, semi-agglutinated to powdery, not fetid spore mass. Spores (Figs. 60 B, C) ovoid to irregularly elongate, sometimes subglobose or lemon-shaped, 12-20 x 17.5-32(-36) μm, when immature hyaline to pale yellowish brown, when mature dark reddish brown, provided with a thin, hyaline sheath and with a long, hyaline appendage, the remains of the sporogenous hypha; wall 1-2 μm thick, excluding the hyaline sheath, which is thick in young, nearly spherical spores but thin in mature ones, spore surface finely, densely foveolate, in LM often appearing as finely reticulate. Hyphae intercellularly, lacking haustoria (Magnus 1900:75, Pl. II). Sterile cells absent. Spore germination (Fig. 60 D) results in holobasidia terminally bearing a large number of fusiform or slightly bent basidiospores which, without conjugation, give rise to hyphae or to short, falciform ballistospores (Brefeld 1895:164-170, Pl. X, figs. 8-21, Săvulescu & Hulea 1955).

On Poaceae: Molinia caerulea (L.) Moench, Phragmites australis (Cav.) Trin. ex Steud. (Ph. communis Trin.); Europe, Asia, N America.

Ref.: Körnicke 1879, Magnus 1900, Bedi, Sikka & Mundkur 1949, Holton 1950('1949'), Săvulescu & Hulea 1955, Khanna & Payak 1968, Patil & Gandhe 1977.

Fig. 60 A-C. Neovossia moliniae on Molinia caerulea, holotype, HUV 9092.

A. Sori in scattered ovaries. Habit (Bar = 1 cm). Enlarged a sorus. **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$). **D**. Germination of spores from *Phragmites australis* (after Săvulescu & Hulea 1955:506).



61. *OBERWINKLERIA* K. Vánky & R. Bauer, *Mycotaxon 53*:363, 1995.

Sori in ovaries of Poaceae, swollen, composed of a peridium of host tissue and of fungal origin, and a central mass of powdery spores. Columella, sterile cells and balls of conidia absent. Spores solitary, pigmented. Spore germination resulting either in relatively few, short and wide basidiospores directly born on pedicels, or in ramified, aseptate hyphae. No evident basidium; this is reduced to the spore. Both basidiospore-like spores and ballistospores are produced on sterigmata on the hyphae. Basidiospores germinate by hyphae or produce ballistospores. Sterile cells absent. Host-parasite interaction by intercellular hyphae, interaction apparatus lacking. Septal pore a dolipore traversed by two membranous plates, pore caps lacking.

Basidia reduced to the teliospores and basidiospores produced on pedicels differentiate this unispecific genus from other genera of the Tilletiaceae family. *Type of the genus*:

Oberwinkleria annulata K. Vánky & C. Vánky,

in Vánky & Bauer, Mycotaxon 53:363, 1995 (as 'anulata').

Tilletia annulata (Vánky & C. Vánky) Piątek, M. Lutz & R. Bauer (in prep.). — Type on *Ortachne erectifolia* (det. H. Scholz), Venezuela, Estado Mérida, c. 50 km E of Mérida, Mts. Cordillera de Mérida, Mt. Sierra Nevada, near Laguna Mucubaj, alt. c. 3500 m, 1.XII.1993, leg. R. Berndt, C. & K. Vánky, HUV 16003! Isotypi in BPI 802368, VEN, VIA and in Vánky, Ust. exs. no. 914.

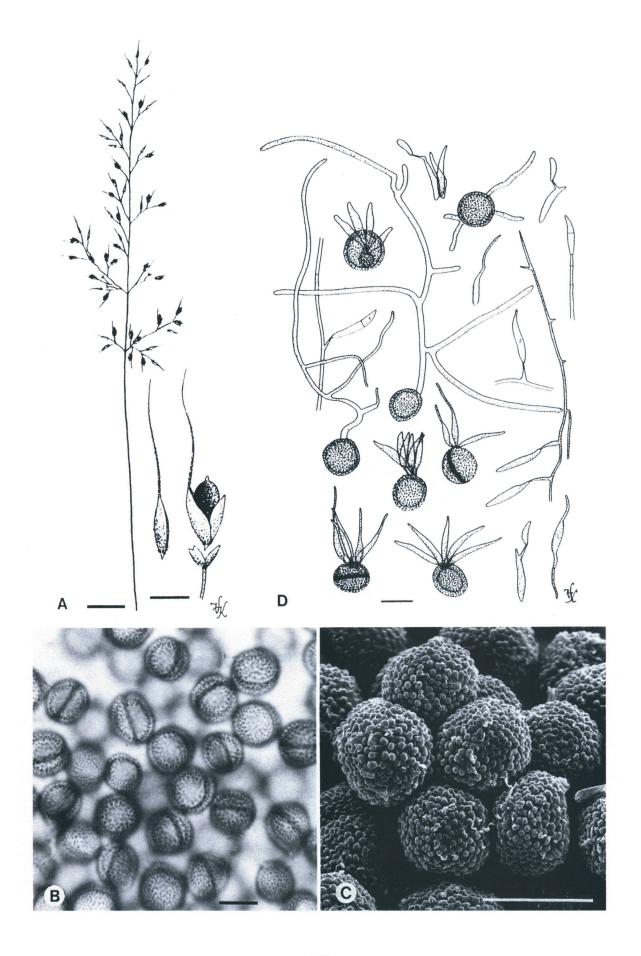
Sori (Fig. 61 A) in some of the ovaries, scattered in the inflorescence, forming ovoid bodies with an acute tip, 0.8-1.2 x 2-3 mm, covered by an initially green later dark brown peridium, usually falling from the host together with, and partly enclosed by the lemma and palea. The peridium is composed of an outer layer of pericarp tissue lined on the proximal part of the sorus by a thin, sporogenous fungal tissue and immature spores. Columella and balls of conidia absent. Spore mass black, powdery, lacking smell of trimethylamine. *Spores* (Figs. 61 B, C) subglobose to ovoid or ellipsoidal, (8-)9-12 x 9-13.5(-14.5) μm, pale, smoky-tinted brown, with an evident, dark blackish brown, narrow (c. 1 μm wide) ring caused by deposition of a dark-colored substance in the external layers of the endospore, in the longitudinal axis of the spores. Spore wall 1-1.5 μm thick, densely, moderately coarsely verrucose. *Sterile cells* absent. *Spore germination* (Fig. 61 D) resulting either in 4-6 basidiospores directly produced on 3-4 μm long pedicels, or in ramified, 1-2 μm thick, aseptate hyphae. No evident basidium; this is reduced to the spore. *Basidiospores* (Fig. 61 D) elongate, 2.5-3 x 10-19 μm, tapering toward each end, often slightly bent, thickest at the proximal 1/3-1/6 part. They germinate without fusion, giving rise to thin (c. 0.5 μm), aseptate, ramified hyphae, or to ballistospores measuring 2.5 x 7-8 μm. Both basidiospore-like spores and ballistospores are born on sterigmata on the hyphae. The basidiospore-like spores produced on hyphae may be one- or two-celled.

On Poaceae: Ortachne erectifolia (Swallen) W.D. Clayton (Muhlenbergia erectifolia Swallen; Lorenzochloa erectifolia (Swallen) J. & C. Reeder); S America. Known only from the type collection.

Ref.: Vánky & Bauer 1995.

Fig. 61 A-D. Oberwinkleria annulata on Ortachne erectifolia, holotype, HUV 16003.

- A. Sori in the ovaries. Habit (Bar = 1 cm). Enlarged a healthy and an infected spikelet (Bar = 1.5 mm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$). Note in B. the typical, dark pigmented, narrow ring of the spores.
- **D.** Spore germination (on WA, at room temp., in 2 weeks, R. Bauer; Bar = $10 \mu m$).



62. ORPHANOMYCES D.B.O. Savile,

Canad. J. Bot. 52:342, 1974.

Sori external on the leaf surface of Cyperaceae (*Carex*) as black, often confluent crusts. Mycelium systemic, perennial. Infected plants do not flower. *Spores* single or in loose balls, moderately large, with brown, coarsely sculptured walls. *Host-parasite interaction* by intracellular hyphae, coated by an electron-opaque matrix. Mature *septa* poreless.

Orphanomyces, tentatively classified in the Anthracoideaceae, has three species: 1. O. hungaricus Vánky & Gönczöl, 2. O. vankyi Savile, in which both the spores are agglutinated in loose but rather persistent spore balls, and 3. O. arcticus (Rostr.) Savile, with single spores. Their taxonomy is far from settled. Very little is known about their germination. The germination type of O. vankyi (Vánky 1987a:84) was quite different from the uncertain germination reported for O. arcticus (Durán & Safeeulla 1968:241). There may be a relationship between Orphanomyces and Clintamra, two genera with rather similar sorus and spore morphology (including germination). Type of the genus:

Orphanomyces arcticus (E. Rostrup) D.B.O. Savile, *Canad. J. Bot.* 52:342, 1974.

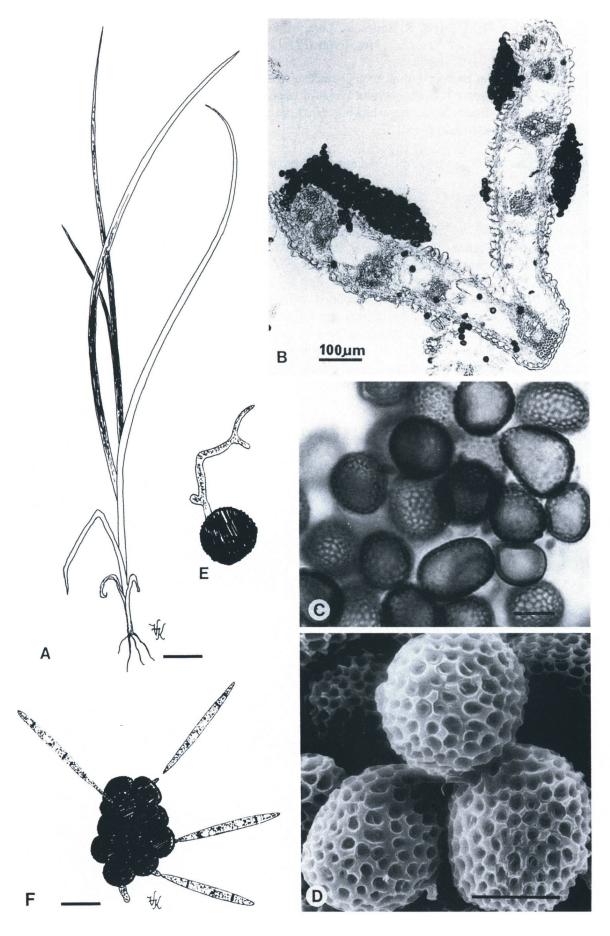
Tilletia arctica Rostrup, Bot. Tidsskr. 15:230, 1886. — Cintractia arctica (Rostr.) Lagerh., in Blytt, Forh. Vidensk.-Selsk. Christiania 1896(6):30, 1896. — Ustilago arctica (Rostr.) B. Lindeberg, Symb. Bot. Upsal. 16:110, 1959. — Type on Carex festiva (= C. macloviana), Norway, Troms, Tromsö, 1885, leg. E. Warming, C. Sori (Figs. 62 A, B) on the surface of young leaves as black, semi-powdery streaks or confluent crusts. Mycelium systemic and perennial in crowns and rhizomes, penetrating the epidermis of young leaves and proliferating between adjacent leaves to produce a coat of spores that are elevated and exposed through the activity of basal meristems. Infected plants do not flower. Spores (Figs. 62 C, D) single, globose, subglobose to ovoid or occasionally somewhat irregular, 11-16 x 13-21 μm, dark reddish brown; wall more or less regularly foveolate-reticulate. Spore germination (Fig. 62 E) results in long, sinuous, septate "promycelia with lateral outgrowths" (Durán & Safeeulla 1968:241).

On Cyperaceae: Carex brunnescens (Pers.) Poiret (C. vitilis Fr.), C. canescens L., C. cinerea Poll., C. davalliana Sm., C. ebenea Rydb., C. eburnea Boott, C. glareosa Wahlenb., C. lachenalii Schkuhr (C. lagopina Wahl.; C. tripartita auct., non All.), C. macloviana d'Urv. (C. festiva Dewey), C. maritima Gunn., C. nubicola Mack., C. scabrizolia Steud., C. stenophylla Wahlenb. (C. duriuscula C.A. Mey.), C. tripartita All.; Europe, Asia, N America.

Ref.: Savile 1974, Vánky & Gönczöl 1978, Vánky 1985a.

Fig. 62 A-D. *Orphanomyces arcticus* on *Carex* sp., Norway, Nordland, Innhavet, 28.VIII.1975, leg. J. Pálsson, HUV 1468.

- A. Sori on the surface of young leaves. Habit (Bar = 1 cm).
- **B.** T.S. of a leaf with the supraepidermal sori.
- C, D. Spores in LM and in SEM (Bars = $10 \mu m$).
- E. Spore germination (in water, at room temp., after several weeks; after Durán & Safeeulla 1968:241).
- **F.** Spore germination of *Orphanomyces vankyi* Savile on *Carex acutiformis* Ehrh., type. (Spores kept previously outdoors during winter, germinated on the surface of a hanging drop of tap-water with a trace of honey, at room temp., after 2-3 weeks). On short, aseptate basidia(?) a long, cylindrical or subfusiform, hyaline, 3(-4)-celled basidiospore(?) is produced measuring 5-5.5 x 70-80 μ m, the further development of which is not known (Bar = 30 μ m).



63. *PARVULAGO* R. Bauer, M. Lutz, M. Piątek, K. Vánky & F. Oberwinkler, *Mycol. Res.* 111:1203, 2007.

Sori as swellings at the base of culms of Cyperaceae (*Eleocharis*), containing a black, agglutinated spore mass. Spores single, pigmented (brown, without violet or reddish tint), embedded in the host tissue. Sterile cells, peridium and columella absent. Septal pore lacking. Host-parasite interaction by intracellular hyphae coated by an electron-opaque vesicular matrix.

Parvulago is a unispecific genus in the Ustilaginaceae family. Type of the genus:

Parvulago marina (M.C. Durieu de Maisonneuve) R. Bauer, M. Lutz, M. Piątek, K. Vánky & F. Oberwinkler, Mycol. Res. 111:1203, 2007.

Ustilago marina Durieu, in Tulasne, Ann. Sci. Nat. Bot. Sér. 5, 5:134, 1866. — Type on Scirpus parvulus (= Eleocharis parvula), France, Dépt. Gironde, Bassin d'Arcachon, near Arès, on sand banks of the ocean, VII.1865, leg. M.C. Durieu de Maisonneuve. Topotype: on VIII.1866, M.C. Durieu de Maisonneuve; isotopotypes in Rbh., Fgi. eur. no. 1199, HUV 4093!, and in Roumeg. Fgi. sel. gall. exs. no. 2352, HUV 12801!

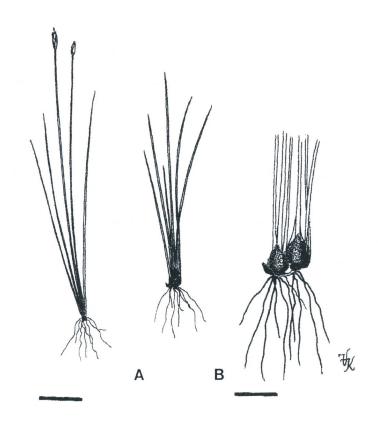
Sori (Figs. 63 A, B) as bullate or onion-shaped, 1-2.5 mm long swellings at the base of culms and basal leaves (like bulbils), containing black, agglutinated spore mass, covered by a thin layer of host tissue. Infection systemic. Spores (Figs. 63 C, D) subglobose, ellipsoidal to slightly irregular, subpolyhedral, $8-13 \times 9-14(-15)$ µm, pale brown; wall 0.5-0.8 µm thick, smooth, often with a few, short, hyaline appendages or thickenings, in SEM surface finely granular to low verruculose. Spore germination unknown.

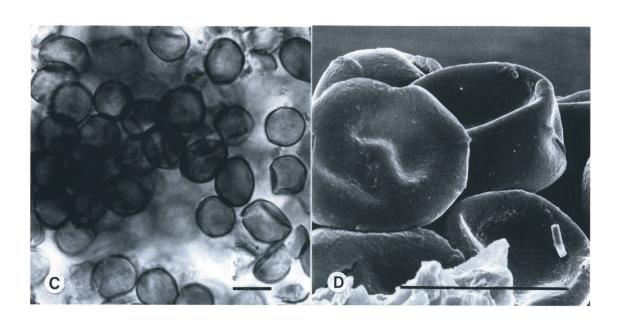
On Cyperaceae: *Eleocharis parvula* (Roem. & Schult.) Link ex Bluff, Nees & Schauer (*Scirpus parvulus* Roem. & Schult.); Europe (Finland, France, Great Britain, Sweden). Certainly more widespread but overlooked.

Ref.: Bauer, Lutz, Piątek, Vánky & Oberwinkler 2007.

Fig. 63 A-D. Parvulago marina on Eleocharis parvula, isotype, Rabenh., Fgi. eur. no. 1199, HUV 4093.

- A. Sori at the base of sterile plants. Habit. Healthy plant (left) (Bar = 1 cm).
- **B**. Sori, enlarged (Bar = 3 mm).
- C, D. Spores in LM and in SEM (Bars = $10 \mu m$).





64. PERICLADIUM G. Passerini,

Nuovo Giorn. Bot. Ital., 7:185, 1875; emend. Mundkur, Mycologia 36:293, 1944a.

XYLOSORIUM Zundel, Mycologia 31:576, 1939. — Type: X. piperis Zundel (as "piperii", = Pericladium piperis (Zundel) Mundkur) on "Piper sp." (= Grewia sp.; Vánky), South Africa. (Syn. by Mundkur 1944a:293).

Sori as pustules or galls on twigs of dicotyledonous plants in Malvaceae (Grewia), formed by a hard, coriaceous peridium of hypertrophied host tissue and hyphae, enclosing dark spore masses, no columella. Spores single, pigmented (brown), powdery at maturity. Sterile cells absent. Spore germination results in ovoid multinucleate holobasidia on short pedicel, giving rise to septate, ramified hyphae on which secondary sporidia develop, or from the spores directly septate, ramified hyphae arise. In nutrient media, germinated spores produce brick-red yeast cultures. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Pericladium, in the Pericladiaceae, Ustilaginales, is one of the very few smut fungi that parasitize woody plants (comp. also *Geminago* and *Uleiella*). It was monographied by Vánky (2011) recognizing 3 species, all on *Grewia*: **1.** *P. piperis* (Zundel) Mundkur from S Africa, **2.** *P. tiliacearum* Mundkur & Thirum. from India, and **3.** The *type of the genus*:

Pericladium grewiae G. Passerini,

Nuovo Giorn. Bot. Ital. 7:185, 1875.

Ustilago grewiae (Pass.) Hennings, Beibl. Hedwigia 39:(75), 1900. — Type on Grewia cf. mollis Juss., Abissinia [= Ethiopia; Eritrea], near Sciotel, Zedamba, VI.1870, leg. O. Beccari.

For the taxonomic synonym *Pericladium flavesci* Prasad & Tyagi see Vánky 2006b:41, and 2011('2012'):464.

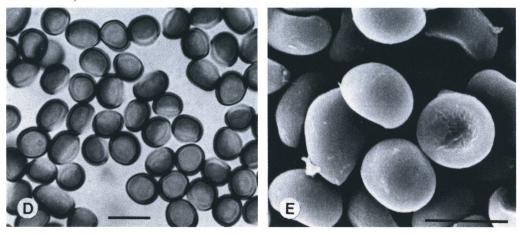
Sori (Figs. 64 A, B, C) on twigs as globose, pustular bodies, c. 1-2 mm in diameter, gregarious to crowded, sometimes entirely surrounding the stems, covered by a brown, coriaceous peridium of hypertrophied host tissue and hyphae. At maturity, the peridium ruptures irregularly revealing the central mass of semi-agglutinated to powdery spores. *Spores* (Figs. 64 D, E) when mature solitary, bun-shaped, more or less flattened on one half, convex on the opposite side, in side view (5-)5.5-7 μm wide, in plane view circular to elliptic, 7-8.5 x 7-10.5 μm, chestnut-brown; wall c. 1 μm thick, on the flattened side pale yellowish brown, thin, c. 0.2 μm, smooth. *Spore germination* (Fig. 64 F), results in one-celled, ovoid holobasidia on a short pedicel, basidium 6-9 x 10-15 μm, with 8-12 nuclei. From the basidia septate, ramified hyphae arise on which secondary, ovoid sporidia develop measuring 3-5.5 x 5.5-8 μm. From the spores directly septate, ramified, 2.5-3.5 μm thick hyphae may arise, similar to those resulting from germinated basidia. Germinated spores produce brick-red yeast cultures.

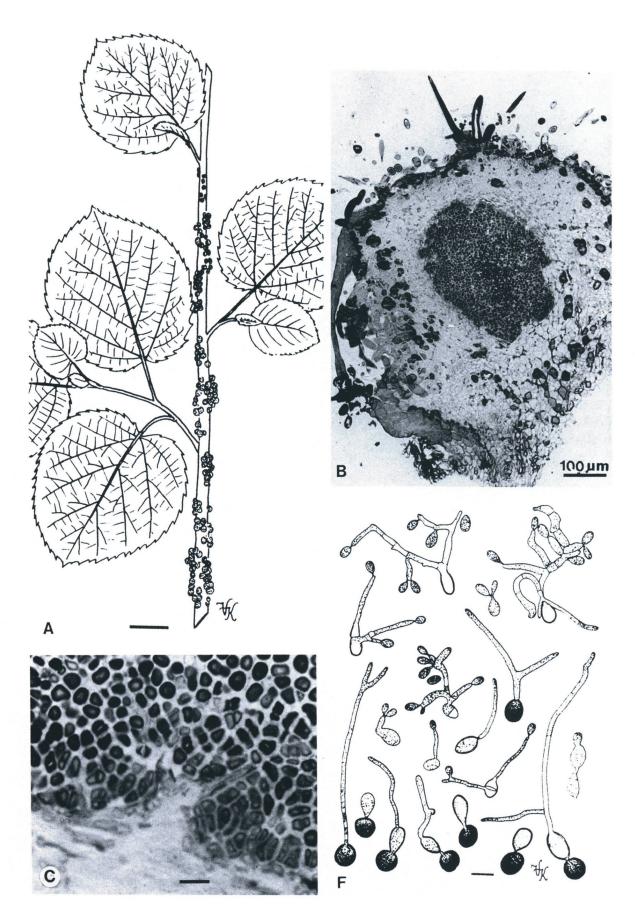
On Malvaceae: At least 12 Grewia species (comp. Vánky 2011); Africa, S Asia, Australia.

Ref.: Hennings 1900, Mundkur 1944a, Thirumalachar 1950b, Ciferri 1954('1953'), Prasad & Tyagi 1961, Vánky 2011b.

Fig. 64 A-E. Pericladium grewiae on Grewia villosa Willd., Vánky, Ust. exs. no. 351, HUV 10725.

A. Sori on the stem forming pustules. **B, C.** T.S. of a young sorus with the central mass of dark spores and the thick, covering host tissue. Enlarged the area of spore formation. **D, E.** Spores in LM and in SEM. **F.** Spore germination (on MYP, at room temp., 2-4 days, R. Bauer) from *Grewia retusifolia* Kurz, Australia, Kununurra, 9.X.1996, A.A. Mitchell; HUV 18334.





65. *PHRAGMOTAENIUM* R. Bauer, D. Begerow, A. Nagler & F. Oberwinkler, *Mycol. Res.* 105:423, 2001.

Sori in the leaves and stems of Poaceae as black spots. Spores single or in groups but not aggregated in balls, pigmented (olive-brown), embedded in the host tissue, not erumpent, not powdery. Spore germination results in phragmobasidia with ballistosporic basidiospores. Host-parasite interaction apparatus lacking. Hyphae mostly intercellular. Septal pore lacking.

Phragmotaenium, in the Tilletiariaceae, so far is a unispecific genus. Certainly, when germination and/or molecular data of further "Melanotaenium" and dark-spored "Entyloma" species on Poaceae are known, the number of Phragmotaenium species will increase. Type of the genus:

Phragmotaenium indicum (K. Vánky, M.S. Patil & N.D. Sharma) R. Bauer, D. Begerow, A. Nagler & F. Oberwinkler, *Mycol. Res.* 105:423, 2001.

Melanotaenium indicum Vánky, M.S. Patil & N.D. Sharma, in Vánky, Mycotaxon 65:149, 1997. — Type on Ischaemum indicum, India, Maharashtra State, Kolhapur, Shivaji University Campus, alt. c. 650 m, 24.X.1995, leg. K. Vánky, HUV 17508!; isotype in HCIO. Topotype: 13.IX.1996, leg. M.S. Patil, Herb. Shivaji Univ., Kolhapur, HCIO, HUV 18032! Paratype: India, Madhya Pradesh, Jabalpur, J.N. Agricultural University Campus, alt. c. 410 m, 27.X.1996, leg. N.D. Sharma, Herb. J.N. Agricult. Univ. Jabalpur, HCIO, HUV 18022!, and in Vánky, Ust. exs. no. 1012.

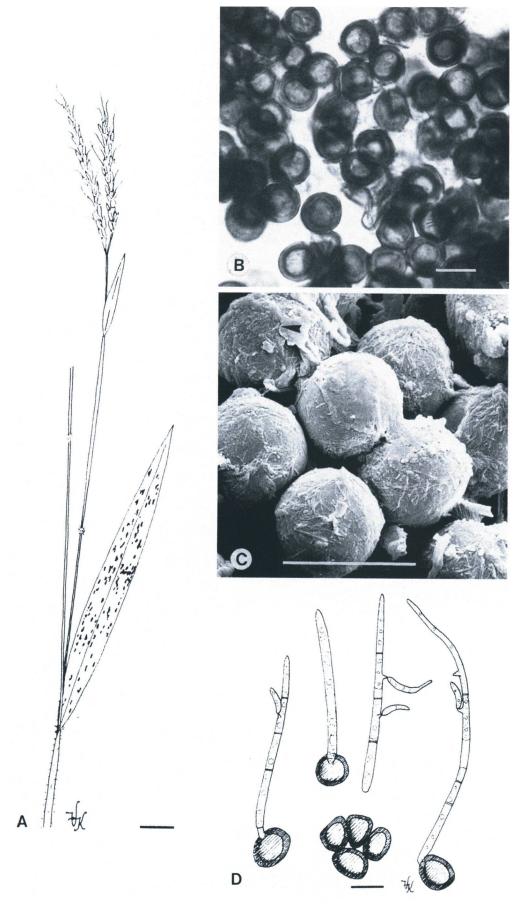
Sori (Fig. 65 A) in leaves forming small, elongate, non-erumpent, black spots, 0.2-0.5 x 0.3-1 mm, or larger by confluence. Spores (Figs. 65 B, C) embedded in the host tissue, subglobose, ovoid, broadly ellipsoidal to slightly irregular, 7-11 x 8-13 μm, olive-brown; wall 1-2.5(-3) μm thick, two-layered, slightly uneven, in LM smooth, in SEM finely, densely verruculose. Spore germination (Fig. 65 D) results in 4-celled phragmobasidia, 2-3 x 50-90 μm. On 1.5-3.5 μm long sterigmata slightly bent ballistosporic basidiospores are produced, 1.5-2 x 8-11 μm. Basidiospores germinate by hyphae.

On Poaceae: Ischaemum indicum (Houtt.) Merrill (I. ciliare Retz.); S Asia (India).

Ref.: Vánky 1997d, Bauer, Begerow, Nagler & Oberwinkler 2001.

Fig. 65 A-D. Phragmotaenium indicum on Ischaemum indicum, holotype, HUV 17508.

- **A.** Sori on a leaf of a flowering plant. Habit (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$).
- **D.** Spore germination (on WA, at room temp., in 5-7 days, stained with cotton blue, R. Bauer; Bar = $10 \mu m$).



66. PILOCINTRACTIA K. Vánky,

Mycol. Balcan. 1:172, 2004.

Sori in some flowers of a spikelet of plants in Cyperaceae (Fimbristylis), forming black, globoid, hard bodies around the nuts, with sterile filaments between the spores. Peridium and stroma may be present. Spores pigmented (brown, without violet or orange-yellow tint), agglutinated, interwoven by hyaline, sterile fungal filaments with protoplasm and gelatinized wall. Spores produced in radially arranged, cup-shaped (in longitudinal section U-shaped) pockets separated by pigmented, tightly packed, sterile fungal cells with a thick, not gelatinized wall, radiating from the basal part of the sori into the spore masses. Spore germination results in phragmobasidia. Basidial cells produce basidiospores or hyphae. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Pilocintractia, tentatively placed in the Anthracoideaceae of the order Ustilaginales, has two known species: **1.** P. adrianae Vánky on Fimbristylis miliacea (L.) Vahl in S & SE Asia (India, Thailand), and **2.** The type of the genus:

Pilocintractia fimbristylidicola (M.S. Pavgi & B.B. Mundkur) K. Vánky, *Mycol. Balcan. 1*:173, 2004.

Cintractia fimbristylidicola Pavgi & Mundkur, Indian Phytopathol. 1:108, 1949 (as 'fimbristylicola'). — Type on Fimbristylis complanata, India, Orissa State, Ganjam, Chatrapur, 30.VIII.1904, leg. E.J. Butler, HCIO 1438; isotypes BPI 171548, HUV 15462!

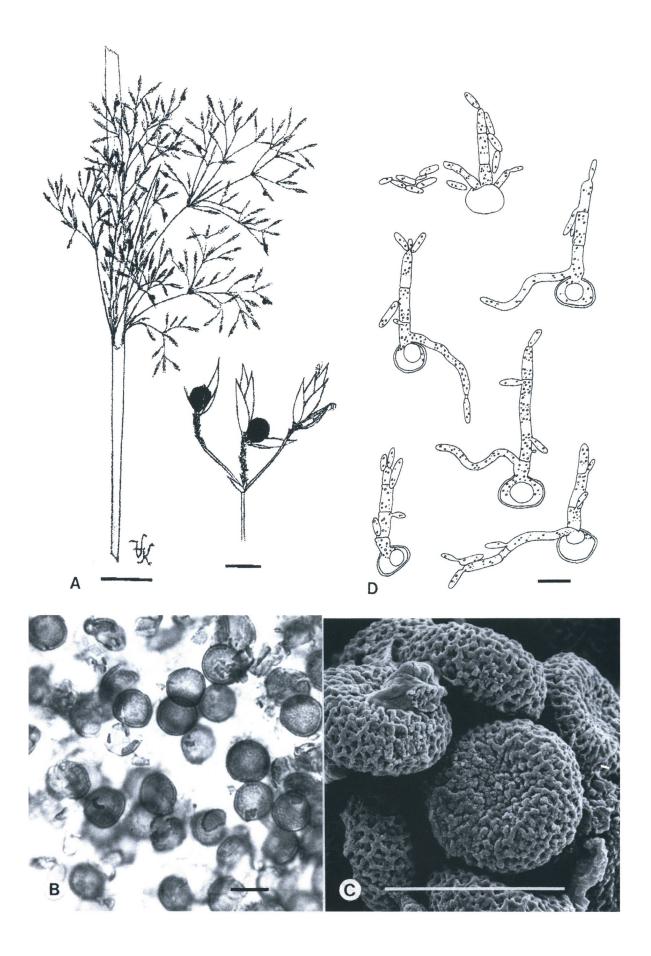
Sori (Fig. 66 A) in some flowers of an inflorescence surrounding the ovaries, black, globoid to ovoid, compact, hard, not powdery, 0.5-1.5 × 1-2 mm, visible between the spreading glumes. Spore mass blackish brown, compact. Peridium absent or weakly developed; basal stroma on the surface of the nuts present or lacking. Spores produced successively in cup-shaped pockets, on the surface of the nuts, delimited by sterile, yellowish brown fungal tissue composed of tightly packed, uniformly thin, c. 1 µm wide, elongate cells. These, in longitudinal section, appear as 15-40 µm wide, c 100-200 µm long, compact fascicles, distally narrowing into a conical tip. Distally from the pockets there is a thick layer of mature spores, permeated by hyaline, sterile hyphae. Long, loose, radially arranged hyaline fascicles of elongate, sterile, fungal filaments also present between the spore masses but usually the filaments are solitary, interweaving the whole mass of mature spores. Filaments 1.5-5 µm wide, with thin, elongate protoplasmic contents and a relatively thick, more or less gelatinized wall, varying in thickness. Spores (Figs. 66 B, C) flattened, in side view elliptic, without hyaline appendages, 6-8 μm wide, in plane view elliptic, ovate or subpolygonally irregular, 8.5-10.5 × 9-12(-13) μm, yellowish brown; wall uniformly 0.5-0.8 μm thick, in LM finely granular-verruculose, spore profile smooth to finely wavy, in SEM warts partly confluent forming a fine to rough, irregular reticulum. Spore germination (Fig. 66 D; Piepenbring 1996:32 & 34, Plate 8) results in phragmobasidia. The cells of the basidia produce basidiospores or hyphae.

On Cyperaceae: Fimbristylis bisumbellata (Forssk.) Bubani, F. complanata Link, F. spadicea (L.) Wahl; S & SE Asia (India, Thailand), Australia, C & S America.

Ref.: Vánky 2004c.

Fig. 66 A, B, C. Pilocintractia fimbristylidicola on Fimbristylis complanata, isotype, HUV 15462.

- **A.** Sori in some flowers of an inflorescence as black, hard not powdery bodies. Habit (Bar = 1 cm), and enlarged two sori (Bar = 2 mm).
- **B, C.** Spores and remnants of sterile, gelatinized fungal filaments in LM and in SEM (Bars = $10 \mu m$).
- **D.** Spore germination (after Piepenbring 1996:34; Bar = $10 \mu m$).



67. PLANETELLA D.B.O. Savile,

Canad. J. Bot. 29:326, 1951.

Sori in and around ovaries of plants in Cyperaceae (*Carex*), forming black, hard bodies, when young invested by a fungal peridium. *Spores* single, subglobose, with a thickened, dark, equatorial band and two, thin-walled, pale-colored, polar areas. *Spore germination* unknown. *Host-parasite interaction* by intracellular hyphae, coated by an electron-opaque matrix. Mature *septa* poreless.

Planetella is a unispecific genus in the Anthracoideaceae, resembling and closely related to Anthracoidea. It is known only on Carex species in the subgenus Vignea. Typical for Planetella is the two, pale-colored, thin-walled polar areas of the spores that are lacking in Anthracoidea. Its transfer into the genus Sphacelotheca (Thirumalachar & Whitehead 1975:85) was an unfortunate proposal. Type of the genus:

Planetella lironis D.B.O. Savile,

Canad. J. Bot. 29:326, 1951.

Sphacelotheca lironis (Savile) Thirumalachar & Whitehead, Sydowia 27:85, 1975. — Anthracoidea lironis (Savile) M. Piepenbring, in Agerer et al. (eds.), Frontiers in Basidiomycote Mycology:159, 2004. — Type on Carex maritima, Canada, Keewatin. Chesterfield Inlet, 23.VIII.1950, leg. D.B.O. Savile 1575 & C.T. Watts, DAOM 25883. Topotype: on 20.VIII.1950, leg. D.B.O. Savile 1559 & C.T. Watts, DAOM 25886; isotopotype HUV 1480! Paratype on Carex leiophylla (= C. sabulosa), Canada, Yukon, Carcross, 13.VII.1949, leg. J.M. Gillett 3772, DAOM 25884.

Sori (Fig. 67 A) in ovaries, scattered in the inflorescence, forming black, hard, rounded bodies around the nutlets, initially invested by a dirty-white, hard fungal peridium that flakes away to expose the black, agglutinated, on the surface semi-powdery spore mass. *Spores* (Figs. 67 B, C) single, subglobose, slightly flattened, 9.5-13.5 μm in polar diameter, 10-15(-16) μm in equatorial diameter; wall with a dark chestnut brown equatorial band, 1.2-2.5 μm thick and 5-7.5 μm wide, and two, pale yellowish brown, thin-walled (c. 0.3 μm) polar regions which in dry spores are depressed, surface in LM apparently smooth or finely punctate, in SEM finely verruculose. *Spore germination* not known.

On Cyperaceae: Carex (subgen. Vignea): C. maritima Gunn. (C. incurva Lightf.) and C. sabulosa Turcz ex Kunth (C. leiophylla Mack.); N America (Canada).

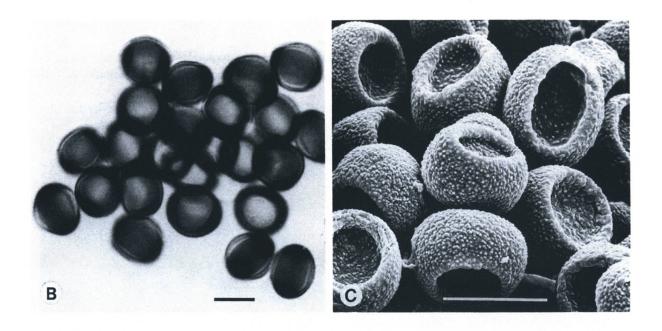
Ref.: Savile 1951.

Fig. 67 A-C. *Planetella lironis* on *Carex maritima*, topotype, 20.VIII.1950, D.B.O. Savile & C.T. Watts, HUV 1480 ex DAOM 25886.

A. Sori in a few ovaries of two inflorescences. Habit (Bar = 1 cm).

B, C. Spores in LM and in SEM. On the SEM picture, the polar, thin-walled areas of the dried spores appear as more or less deep depressions (Bars = $10 \mu m$).





68. *PORTALIA* V. González, K. Vánky & G. Platas, in González, Vánky, Platas & Lutz, *Fungal Diversity 27*:54, 2007.

Sori in the flowers of Cyperaceae (*Scirpus*), peridium lacking, spore mass black, when mature powdery, composed of spores only, no sterile cells. Infection systemic. *Spores* single, pigmented (brown), ornamented. *Spore germination* results in septate basidium producing hyphae which may fuse.

Portalia is so far a unispecific genus, probably in the Anthracoideaceae. Type of the genus:

Portalia uljanishcheviana (S.R. Schwarzman) V. González, K. Vánky & G. Platas, in González, Vánky, Platas & Lutz, *Fungal Diversity 27*:54, 2007.

Cintractia uljanishcheviana Schwarzman, Fl. spor. rast. Kazakhstana 2:162, 1960 (as 'uljanishchevianum'). — Anthracoidea uljanishcheviana (Schwarzman) M. Piepenbring, Nova Hedwigia 70:362. — Type on Holoschoenus vulgaris (= Scirpus holoschoenus), Kazakhstan, Dzhambulskaya Obl., Ul'kun-Burul, Lake Bijlikul, 12.VII.1949, leg. S.R. Schwarzman, AA; isotype HUV 12116!

Sori (Fig. 68 A) in the flowers, usually affecting all in a spikelet, destroying the innermost floral organs replacing them with a black, semi-agglutinated to powdery mass of spores completely hidden by the outermost floral envelopes. Peridium and stroma lacking. Infected spikelets swollen, globoid or ovoid, 1-2 mm in diameter Infection systemic; all spikelets (or nearly all) of a head, and all heads of an inflorescence are affected. *Spores* (Figs. 68 B, C) single, subglobose, ovoid, ellipsoidal, elongate or irregular, sometimes with a short subacute tip and also with a short, hyaline papilla, 10.5-15 × 12-18.5 μm, reddish or olivaceous brown; wall even to slightly uneven, 0.5-1(-1.5) μm thick, finely to coarsely verrucose, warts isolated or often connected by low ridges forming a fine, irregular and incomplete reticulum, as seen in SEM. Spore profile in LM wavy to finely, bluntly serrulate. *Spore germination* (Fig. 68 D; González *et al.* 2007:58, fig. 4) results in a 4-celled basidium. After conjugation of compatible basidial cells, long, dikaryotic, ramifying hyphae with retraction septa are produced.

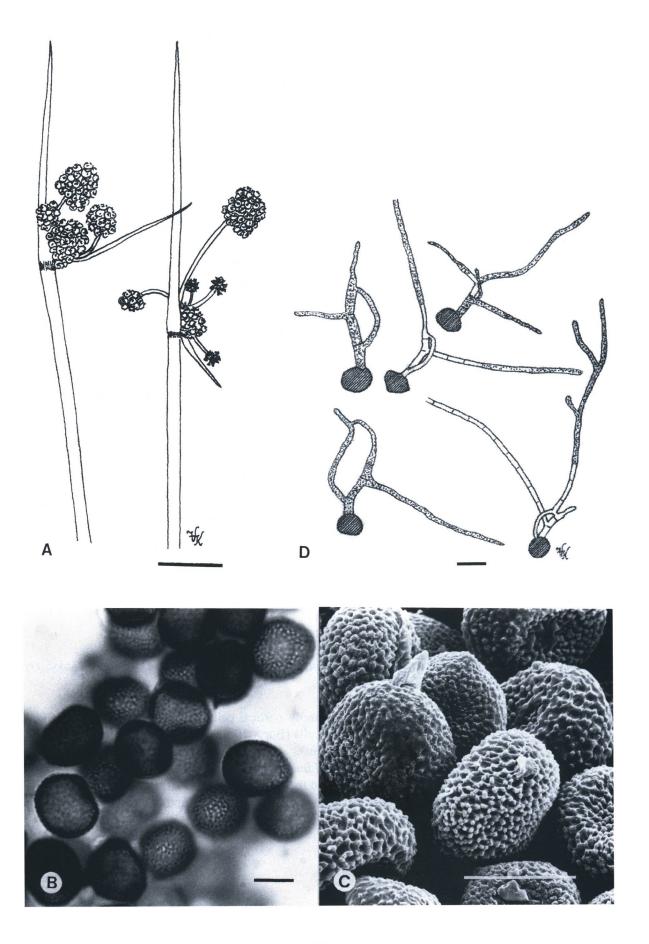
On Cyperaceae: Scirpus holoschoenus L. (Holoschoenus vulgaris Link); Europe (Spain), Asia (Kazakhstan).

Piepenbring (2000:362) considered Cintractia uljanishcheviana to be an Antracoidea species.

Ref.: González, Vánky, Platas & Lutz 2007.

Fig. 68 A-C. Portalia uljanishcheviana on Scirpus holoschoenus, isotype, HUV 12116;

- **D.** From Spain, Cuenca Prov., Huete, road CM 2025 Sacedón-Huete, Arroyo Valquemado, 8.VIII.2006, V. González, HUV 21372.
- **A.** Sori in the flowers of two inflorescences, forming black, hard, not powdery bodies, hidden by the outermost floral envelopes. Habit (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$).
- **D.** Spore germination (on WA, at room temp., in 2-3 days; Bar = $10 \mu m$).



69. PSEUDODERMATOSORUS K. Vánky,

Mycotaxon 71:213, 1999.

Sori in leaves of aquatic or paludal plants (in Alismataceae) as yellowish brown spots with spore balls embedded in the host tissue. *Spore balls* permanent, composed of a cortex of sterile cells and a central mass of poorly pigmented spores embedded in a network of sterile fungal cells. *Host-parasite interaction* by complex interaction apparatus with cytoplasmic portions, haustoria absent. *Septal pore* simple, with two membrane caps.

Pseudodermatosorus belongs to the Doassansiaceae, together with Burrillia, Doassansia, Entylomaster, Doassinga, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodoassansia, Pseudotracya and Tracya. It has two known species, both on Alismataceae: 1. P. sagittariae (Vánky & C. Vánky) Vánky on Sagittaria planitiana Agostini, from Venezuela, and 2. The type of the genus:

Pseudodermatosorus alismatis-oligococci (K. Vánky) K. Vánky,

Mycotaxon 71:215, 1999.

Doassansia alismatis-oligococci Vánky, Svensk Bot. Tidskr. 69:45, 1975. — Type on Alisma oligococcum (= Caldesia oligococca), Sri Lanka, Yala National Park, alt. c. 15 m, 12.III.1974, leg. K. Vánky, S; isotypes in UPS, IMI 190442, HUV 472!, and in Vánky, Ust. exs. no. 176 (as Doassansia alismatis-oligococci).

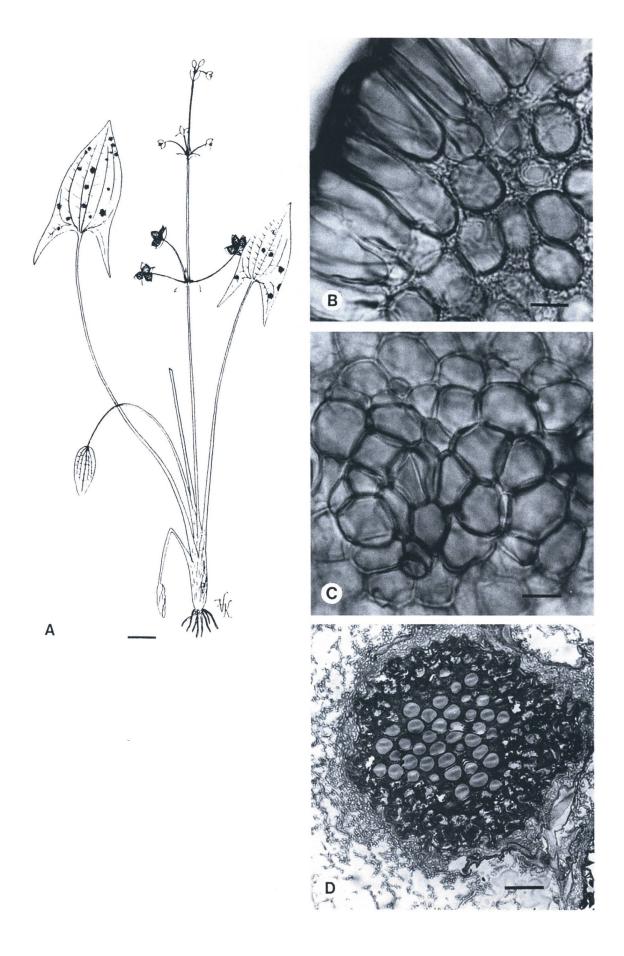
Sori (Fig. 69 A) in leaves, forming initially pale yellow, later brown, small, scattered or grouped, circular, amphigenous spots or pustules, 1-4(-5) mm in diameter, with subepidermal spore balls visible as minute, brown, punctate elevations or pustules when numerous and grouped. Spore balls (Figs. 69 B, D) permanent, globose, ovoid, elongate or irregular, 100-230 x 150-300 μm, pale brown, each composed of a cortical layer of sterile cells and a core of numerous spores embedded in a very fine, subhyaline network of sterile fungal cells. Cortical sterile cells (Figs. 69 B, C) in one layer, in surface view very varying in shape and size, rounded, elongate, polygonal, 4-18 x 6-22 μm, in side view radially elongate, subquadrangular to subtriangular, firmly adhering to each other, 7-20 x 10.5-36 μm, pale yellowish brown or subhyaline; wall 0.8-1.5 μm thick, smooth. Spores (Fig. 69 B) more or less globose, ovoid, rarely slightly irregular, 9.5-13.5 x 10.5-17.5 μm, pale yellowish brown or subhyaline; wall c. 0.8 μm thick, smooth. The space between the spores varies between 0-12(-16) μm and is filled with a very fine, subhyaline network of sterile fungal cells. The young spore balls (Fig. 69 D) are surrounded by a thick mycelial layer. Thin-walled spore initials, scattered in an apparently structureless, central fungal mass are formed. In this stage of spore ball development no network of small, empty, fungal sterile cells between the spores, and also no cortical layer of sterile cells can be seen. They differentiate later.

On Alismataceae: *Caldesia oligococca* (F. Muell.) Buchenau (*Alisma oligococcum* Mueller; *A. glandulosum* Thw.), *Limnophyton obtusifolium* (L.) Miq.; Africa (South Africa, Zimbabwe), S Asia (Sri Lanka).

Ref.: Vánky 1975, 1999c.

Fig. 69 A-C. Pseudodermatosorus alismatis-oligococci on Alisma oligococcum, isotype, Vánky, Ust. exs. 176 (as Doassansia alismatis-oligococci), HUV 472.

- A. Sori in the leaves. Habit (Bar = 1 cm).
- **B.** Part of a hand-sectioned spore ball with elongate, empty cortical cells, and subglobose to ellipsoidal, thin-walled spores scattered in a very fine network of fungal cells (Bar = $10 \mu m$).
- C. Cortical, sterile cells seen in surface view (Bar = $10 \mu m$).
- **D.** Developing spore ball of *P. alismatis-oligococci* on *Limnophyton obtusifolium* (HUV 18509) with a central mass of young spores, an undeveloped cortex and around the spore ball a layer of hyphae. No network of small, empty, sterile fungal cells can be seen between the spores in this stage of development (Bar = $25 \mu m$).



70. PSEUDODOASSANSIA (W.A. Setchell) K. Vánky,

Sydowia 34:174, 1981; emend. Vánky, Mycotaxon 78:274, 2001.

DOASSANSIA Cornu subgen. PSEUDODOASSANSIA Setchell, Proc. Amer. Acad. Arts 26:16, 1891.

Sori forming spots on aquatic or paludal plants (in Alismataceae and Limnocharitaceae) with spore balls embedded in the host tissue. Spore balls rather permanent, composed of a cortex of sterile cells and a network of branched hyphae in which the spores are scattered irregularly or concentrated towards the periphery of the balls. Spores pale-colored (subhyaline or pale yellowish brown). Spore germination of Tilletia-type. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore is simple, with two membrane caps.

Pseudodoassansia belongs to the Doassansiaceae, together with Burrillia, Doassansia, Entylomaster, Doassinga, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudotracya and Tracya. It has two known species: 1. P. hydrocleydis Vánky on Hydrocleys nymphoides (Willd.) Buchenau (Limnocharitaceae), from Argentina, and 2. The type of the genus:

Pseudodoassansia obscura (W.A. Setchell) K. Vánky,

Sydowia 34:175, 1981.

Doassansia obscura Setchell, Proc. Amer. Acad. Arts 26:16, 1891. — Lectotype on Sagittaria variabilis (= S. sagittifolia), USA, (design. by Vánky 1981b:175) Massachusetts, Cambridge, IX.1890, leg. W.A. Setchell, BPI 178468; isolectotypes in DAOM, H, HMAS, PC, HUV 9072!

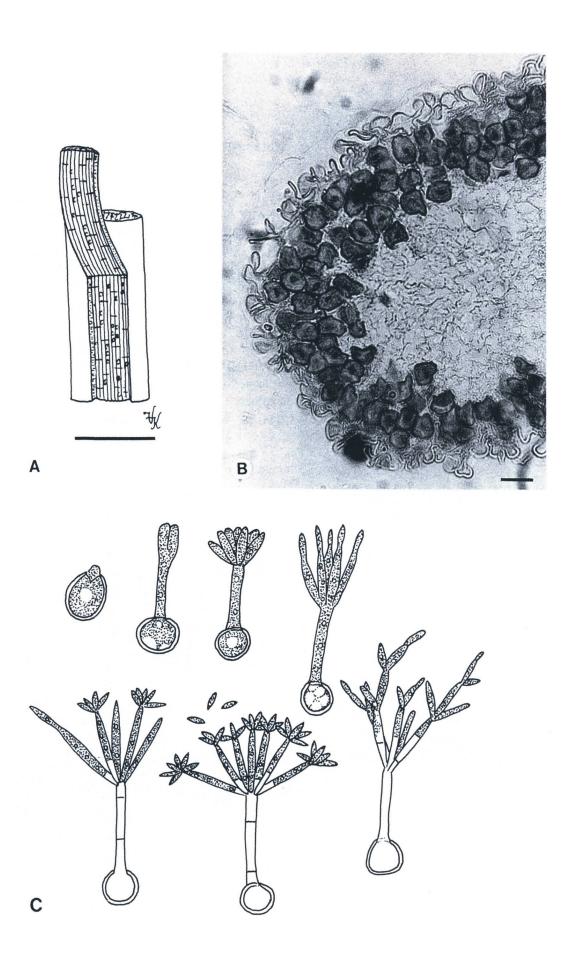
Sori (Fig. 70 A) on the basal part of the petioles as inconspicuous, pale yellowish green spots or on the white portions of petioles as thin, brown striae with spore balls embedded in the host tissue. Spore balls (Fig. 70 B) rather permanent, globose, ovoid or slightly irregular, 180-220 x 200-300 μm, pale brown, composed of a central network of fine, branched hyphae, surrounded by several layers of loosely arranged spores and a distinct cortical layer of sterile cells. Spores (Fig. 70 B) globose to subglobose, 8-12 μm in diameter, subhyaline to pale yellowish brown, with smooth, c. 0.5 μm thick wall. Cortical cells (Fig. 70 B) irregular, often deeply lobed (collapsed), pale brown colored. Spore germination (Fig. 70 C) results in a cylindrical, c. 20 μm long, aseptate basidium bearing a terminal whorl of 5-7 basidiospores, 1.5-2 x 16-17 μm, producing secondary sporidia without conjugation (Setchell 1892:43).

On Alismataceae: Sagittaria sagittifolia L. (S. latifolia Willd.; S. variabilis Engelm.); N America. Known only from the type collection. Probably more common but overlooked, due to the inconspicuous sori.

Ref.: Setchell 1891, 1892, Vánky 1981b, 2001c.

Fig. 70 A-C. Pseudodoassansia obscura on Sagittaria sagittifolia, isolectotype, HUV 9072.

- **A.** Sori in a piece of leaf petiole (enlarged). A strip of the epidermis is removed to show the spore balls embedded in the host tissue as small, pale brown dots.
- **B.** T.S. of a part of a spore ball with an outer, cortical layer of irregular, pale brown, sterile cells. Between the cortex and a central network of fine, branched hyphae, several layers of dark (stained), loosely arranged spores can be seen.
- C. Spore germination (after Setchell 1892).



71. PSEUDOTRACYA K. Vánky,

Mycotaxon 71:216, 1999.

Sori forming spots in vegetative parts of aquatic plants (Hydrocharitaceae). Spore balls embedded in the host tissue, visible as minute, brown dots. Spore balls composed of a cortex of fertile spores and a central mass of sterile, parenchymatous fungal tissue; an external layer of sterile cells is lacking. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore simple, with two membrane caps.

Pseudotracya belongs to the Doassansiaceae, together with Burrillia, Doassansia, Entylomaster, Doassinga, Heterodoassansia, Nannfeldtiomyces, Narasimhania, Pseudodermatosorus, Pseudodoassansia and Tracya. Currently it is a unispecific genus. It differs from Tracya H. & P. Sydow in the structure of the spore balls. In Pseudotracya the spore balls are filled with a parenchymatous fungal tissue, whereas in Tracya they are filled with a network of branched, septate, hardened hyphae. Type of the genus:

Pseudotracya otteliae K. Vánky,

Mycotaxon 71:216, 1999.

Type on *Ottelia ovalifolia*, Australia, Queensland, c. 160 km W of Rockhampton, Blackdown Tableland, Stony Creek, 3.IX.1974, leg. A.B. Cribb, BRIP 8026; isotype HUV 18534!

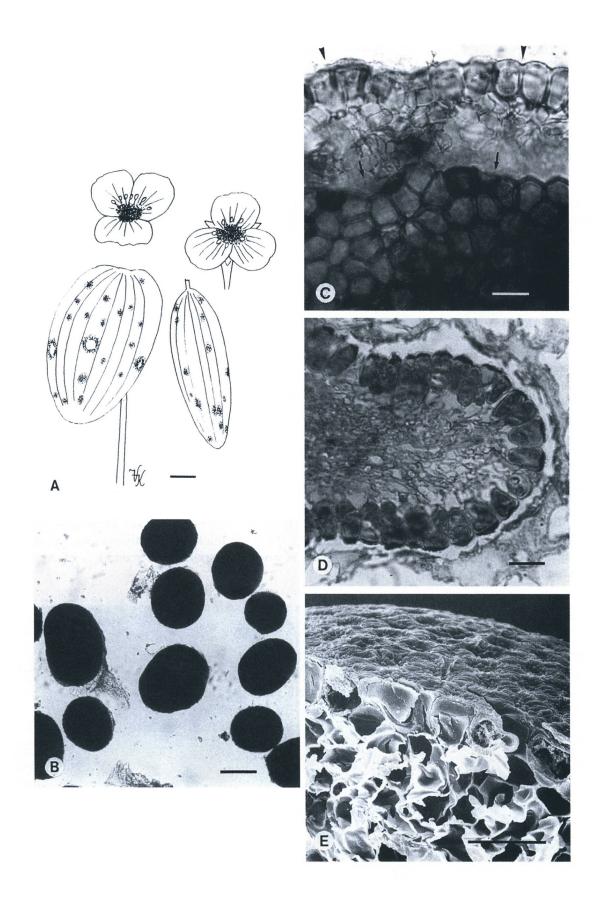
Sori (Fig. 71 A) in leaves forming indistinct, yellow to yellowish brown spots, 2-10 mm in diameter, with spore balls embedded in the host tissue appearing as minute, brown, slightly elevated dots. Old sori often perforated due to destroyed host tissues. Spore balls (Figs. 71 B, C, D, E) persistent, globose, ovoid, elongate, 80-170 x 110-220(-270) μm, pale brown, composed of a cortical layer of firmly adhering spores and a central mass of parenchymatous fungal tissue. Spores (Figs. 71 C, D, E) in surface view polyangularly irregular, (5-)6-9.5 x (5-)6-12 μm, verrucose, in side view subquadrangular or radially elongate, subtetrangular, rarely subtriangular, 4-9 x 10-13 μm, pale yellowish brown; outer, free, verrucose wall 1.5-2.5 μm thick, contact and inner walls thin, c. 0.5 μm, smooth. Central mass of parenchymatous tissue (Figs. 71 C, D, E) composed of empty cells, extremely varying in shape and size, 2.5-8 x 5-15 μm, pale yellowish brown; wall thin, c. 0.4 μm, smooth. Spore germination not known.

On Hydrocharitaceae: Ottelia ovalifolia (R.Br.) Rich.; Australia. Known only from the type collection.

Ref.: Vánky 1999c.

Fig. 71 A-E. Pseudotracya otteliae on Ottelia ovalifolia, isotype, HUV 18534.

- A. Sori on the leaves and two flowers. Habit. (Bar = 1 cm).
- **B.** Spore balls in LM (Bar = $100 \mu m$).
- C. A broken spore ball showing the cortical layer of spores in median view (arrow heads) and in superficial view (arrows). Between them, the paler colored mass of the central, parenchymatous sterile cells can be seen (Bar = $10 \mu m$).
- **D, E.** Sectioned spore balls in LM and in SEM showing the single layer of peripheral, tightly adhering spores (colored in D), and the empty, more or less collapsed cells of parenchymatous fungal tissue filling the spore balls (Bars = $10 \mu m$).



72. RESTIOSPORIUM K. Vánky,

Mycotaxon 74:346, 2000.

Sori in fruits of plants in the Restionaceae s. lat. (incl. Anarthriaceae and Lyginiaceae), replacing the seeds with a black, granular powdery mass of spore balls differentiating within a mass of sporogenous hyphae. Attacked male plants develop gynoecia with sori (transvestitism). Spore balls composed of spores only. Peridium, columella and sterile cells absent. Spores pigmented (brown). Spore germination (where known) results in 4-celled phragmobasidia in which basidial cells fuse in pairs. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Restiosporium, in the Websdaneaceae of the order Ustilaginales, contains 21 known species in Australia and New Zealand. It is interesting that not a single smut fungus (excepting for the ascomycetous Restilago capensis) has been found in South Africa which has almost twice as many species of Restionaceae (c. 320) as there are in Australia (c. 170). Restiosporium appears to represent a phylogenetically young group in terms of its speciation and radiation. It was monographied by Vánky (2006a). Type of the genus:

Restiosporium meneyae K. Vánky,

Mycotaxon 74:347, 2000.

Type on *Lyginia barbata*, Australia, Western Australia, c. 200 km N of Perth, Dandaragan Distr., Brand Hwy between Cataby Roadhouse et Badgingarra, alt. c. 200 m, 30.I.1996, leg. K. Websdane, C. & K. Vánky, HUV 17938!; isotypes BRIP 27418, PERTH 7534620, and in Vánky, Ust. exs. no. 1075. Paratypi: idem, 25.II.1992, leg. K. Meney, UWA, HUV 17161!; Western Australia, 19 km SE of Perth, XI.1992, leg. K. Meney, UWA, HUV 17162!; Western Australia, Albany Distr., 15 km S of Albany, Torndirrup National Park, alt. c. 150 m, 11.II.1996, leg. C. & K. Vánky, PERTH, HUV 17940!

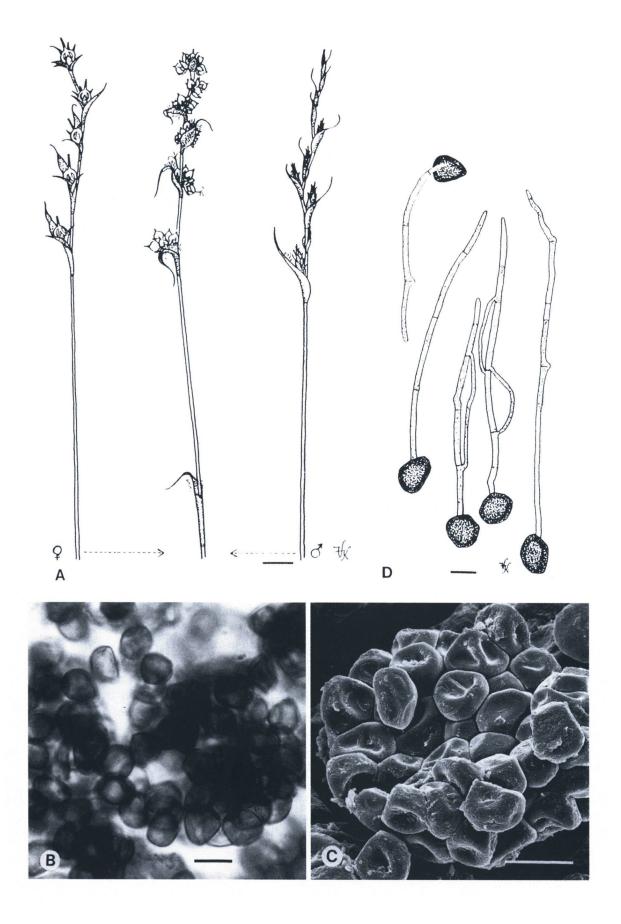
Sori (Fig. 72 A) inconspicuous, filling the capsules with a black, granular-powdery mass of spore balls. Infected male plants develop capsules with spores (transvestitism). Infection systemic, all flowers of a plant being affected. Infected capsules smaller and more numerous per culm than those of healthy female plants. Spore balls (Figs. 72 B, C) varying in shape and size, ovoid, elongate or irregular, 40-70(-80) x 50-100(-120) μm, dark olivaceous brown, composed of many (tens to hundreds), easily separating spores. Spore balls developing from concentrated groups of sporogenous hyphae within a hyaline mass of hyphae. Spores (Figs. 72 B, C) varying in shape and size, subglobose, ovoid, elongate, usually subpolyhedrally or polyhedrally irregular, 7-10 x 9-14 μm, olive-brown; wall uniformly 0.5-1 μm thick, apparently smooth, in LM often with acute edges showing as lines on the spore surface when the spores are seen in surface view. Spore germination is not known.

On Lyginiaceae (Restionaceae s. lat.): Lyginia barbata (Labill.) R.Br., Australia.

Ref.: Websdane 1995, Vánky 2000b, 2006a, Vánky & McKenzie 2002a.

Fig. 72 A-C. Restiosporium meneyae on Lyginia barbata, holotype, HUV 17938.

- **A.** Sori in the capsules. Habit. Healthy female plant (left), healthy male plant (right), infected female or male plant (transvestitism) with capsules filled with spore balls replacing the seeds (center). (Bar = 1 cm).
- **B, C.** Spore balls and spores in LM and in SEM (Bars = $10 \mu m$).
- **D.** Germinating spores of *Restiosporium lepidoboli* (McAlp.) Vánky on *Lepidobolus chaetocephalus* F. Mueller ex Benth. (on WA, at room temp., after 3 weeks, R. Bauer; HUV 17979; Bar = 10 μm).



73. RHAMPHOSPORA D.D. Cunningham,

Sci. Mem. Off. Med. Dept. Gov. India 3:32, 1888('1887').

Sori in leaves and stems of aquatic plants in Nymphaeaceae, forming spots. Spores embedded in the host tissue, solitary, pale, usually lemon-shaped with a papilla at one end and a short hyphal appendage at the opposite end, produced subterminally on branches of sporogenous hyphae. Spore germination results in aseptate basidia on which 4-6 apical basidiospores are produced. Basidiospores giving rise to secondary and tertiary, fusiform sporidia, perpendicular to the long axis of the basidiospores. Host-parasite interaction (Fig. 5, p. 23) by complex interaction apparatus with cytoplasmic portions in the hyphae and haustoria. Hyphae intercellular, septate, with clamp connections, binucleate, with intracellular, ramified haustoria. Septal pore simple, with two membrane caps. Type of the genus: R. nymphaeae.

Rhamphospora is a unispecific genus in the Rhamphosporaceae of the Doassansiales. Because of the pale colored, solitary spores embedded in the host tissue, it was merged with *Entyloma* by some authors. However, the two genera are not related.

Rhamphospora nymphaeae D.D. Cunningham, s. lat.,

Sci. Mem. Med. Off. Army India 3:32, 1888('1887'),

Entyloma nymphaeae (D.D. Cunningham) Setchell, Bot. Gaz. (Crawfordsville) 19:189, 1894. — Lectotype on Nymphaea (design. by Vánky 1987a:94) stellata (= N. nouchali), India, Calcutta, Botanical Garden, autumn 1886, leg. D.D. Cunningham.

Taxonomic synonyms are: *Entyloma castaliae* Holway on *Nymphaea* species, *Entyloma dubium* Cif., on *Nuphar advena* (= *Nymphaea advena*), and *Entyloma nymphaeae* (D.D. Cunn.) Setch. var. *macrospora* Thirum., Pavgi & Safeeulla on *Nymphaea* sp. (comp. Vánky, *Smut Fungi of the World*, 2011('2012'):493).

Sori (Fig. 73 A) in leaves as scattered or gregarious, initially pale yellow, later brown spots, round or by confluence irregular, often perforated with age. Spores (Figs. 73 C, D) embedded in the host tissue, subglobose to ovoid, usually lemon-shaped, papillate at one end (1-2 μm high) and appendiculate at the other end from remnants of the sporogenous hypha, 7-11 x 8-14 μm, hyaline or pale yellow; wall c. 1.5 μm thick, smooth or finely, densely verruculose. Spores formed subterminally on the branches of ramified sporogenous hyphae (Fig. 73 B), especially in the large air-canals but also in any free space between cells of the leaf. Spore germination (Fig. 73 E): Mature spores germinate without resting period, often while the leaf is still alive. An aseptate basidium produces 4-6 apical, fusiform, often slightly bent basidiospores on short sterigmata. On the basidiospores, with 2-3 retraction(?) septa, c. 0.9 μm wide and up to 21 μm long, fusiform, secondary sporidia are produced on short pedicels, perpendicular to the long axis of the basidiospores. Secondary sporidia may produce tertiary sporidia, in the same way, or secondary sporidia conjugate in pairs by a short or long conjugation bridge (see Cunningham 1888('1887'):29-30 & Pl. II). Hyphae intercellular, septate, with clamp connections, binucleate, branching, with well-developed, intracellular, ramified, binucleate haustoria (Lutman 1910:1216, figs. 63-71). Anamorph not observed.

On Nymphaeaceae: Castalia reniformis (Walter) Nash, Nymphaea advena Aiton (Nuphar advena (Aiton) W.T. Aiton), Ny. alba L., Ny. alba var. rubra Lönnr., Ny. ampla (Salisb.) DC., Ny. capensis Thunb., Ny. lotus L., Ny. lotus var. pubescens (Willd.) Hook. fil. (Ny. pubescens Willd.), Ny. marliacea hort. (cult.), Ny. nouchali Burm. fil. (Ny. caerulea Savigny; Ny. stellata Willd.), Ny. odorata Aiton (Castalia odorata (Aiton) Wood; Ny. reniformis Walter), Ny. tetragona Georgi, Ny. tuberosa Paine (Castalia tuberosa (Paine) Greene); cosmopolitan.

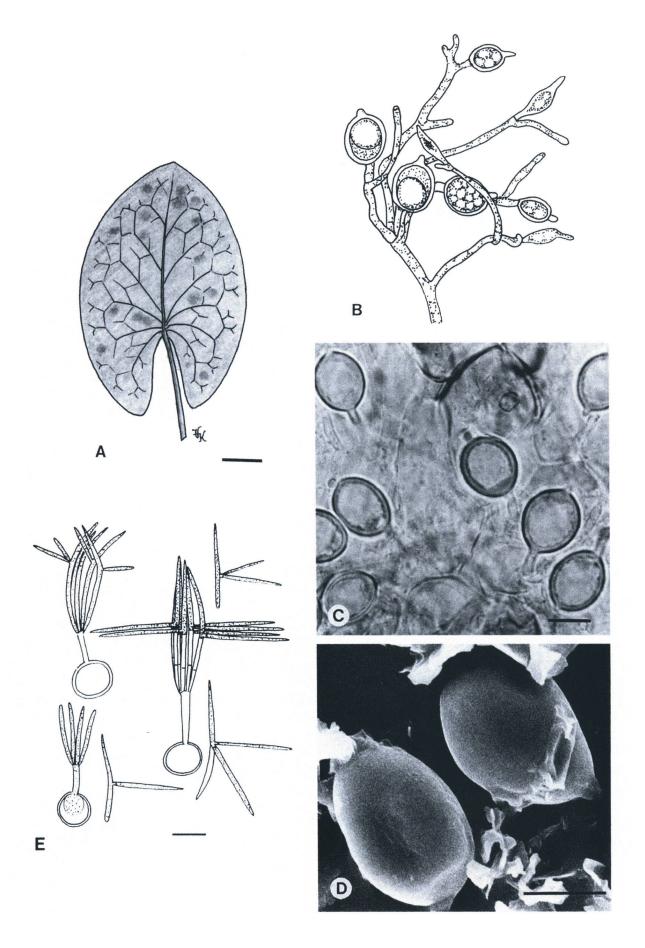
Ref.: Cunningham 1888, Lutman 1910, Liro 1938, Vánky, Bauer & Begerow 1998.

Fig. 73 A-D. Rhamphospora nymphaeae on Nymphaea stellata Willd. A, C, D. Vánky, Ust. exs. no. 182, HUV 5359.

A. Sori on a leaf forming circular, darker spots of variable size. Habit (Bar = 1 cm). **B.** Spore formation (after Cunningham 1888, Pl. II).

C, D. Spores in LM and in SEM (Bars = $10 \mu m$).

E. Germination of spores from *Nymphaea alba* L. (on WA, at room temp., in 2 days, R. Bauer; Bar = $10 \mu m$).



74. *SALMACISIA* D.R. Huff & A. Chandra, in Chandra & Huff, *Mycologia 100*:91, 2008.

Sori in ovaries of plants in Poaceae filled with semi-agglutinated spore mass mixed with sterile cells. Spores single, pigmented (yellowish brown), ornamented and with a gelatinous sheath. Morphologically indistinguishable from species of Tilletia. Spore germination of Tilletia-type. Type of the genus: S. buchloëana.

Salmacisia differs from the genus *Tilletia* by its molecular phylogenetic characters only, based solely on nLSU-rDNA sequence diversity (= cryptic genus).

Salmacisia buchloëana (W.A. Kellerman & W.T. Swingle) D.R. Huff & A. Chandra, in Chandra & Huff, *Mycologia 100*:91, 2008.

Tilletia buchloëana Kellerman & Swingle, *J. Mycol.* 5:11, 1889. — Syntypes on *Buchloë dactyloides*, USA, Kansas, Trego Co., 1886, and Kansas, Ford Co., Bucklin, 26.VI.1888, FH, BPI 172559.

Ustilago cathesteci Hennings, Hedwigia 36:212, 1897. — Tilletia cathesteci (Henn.) G.P. Clinton, J. Mycol. 8:149, 1902. — Type on Cathestecum procumbens, Mexico, without date and locality, leg. K. Schumann, BPI 172669. (synonymy supposed by Clinton 1904:440, confirmed by Durán & Fischer 1961:41).

Sori (Figs. 74 A, B) in all ovaries of an infected plant, ovoid or lemon-shaped, c. 1 × 1.5-2 mm, more or less hidden by the floral envelopes and covered by the thin, brown pericarp that ruptures irregularly at maturity, disclosing the reddish brown, semi-agglutinated to powdery mass of spores and sterile cells, with typical smell of trimethylamine. Infection systemic. Infected plants have denser and darker inflorescences with spreading glumes. *Spores* (Figs. 74 C, D) rather uniform, globose, subglobose to broadly ellipsoidal, 17.5-20(-21) × 18-22(-24) μm, including the 2-3 μm high sheath, pale yellowish brown; wall provided with inconspicuous, pale colored, blunt, subpyramidal tubercles about the height of the subhyaline or pale yellowish brown sheath or somewhat shorter, 19-28 on the spore circumference. In SEM spore surface slightly undulate, smooth (due to the sheath). *Sterile cells* (Figs. 74 C, D) globose, ovoid to irregular, 8-20 × 10.5-21 μm, hyaline, content granular, yellowish, often very much reduced; wall 2.5-7 μm thick, multilayered. *Spore germination* (Fig. 74 E; Durán 1987:151, pl. 69, figs. C, D, pl. 70, fig. E; Chandra & Huff 2008) results in multinucleate holobasidia, simple or branched, with an apical whorl of mono- or binucleate basidiospores. The mononucleate basidiospores fuse in pairs developing hyphae and secondary sporidia, like those produced by the binucleate basidiospores.

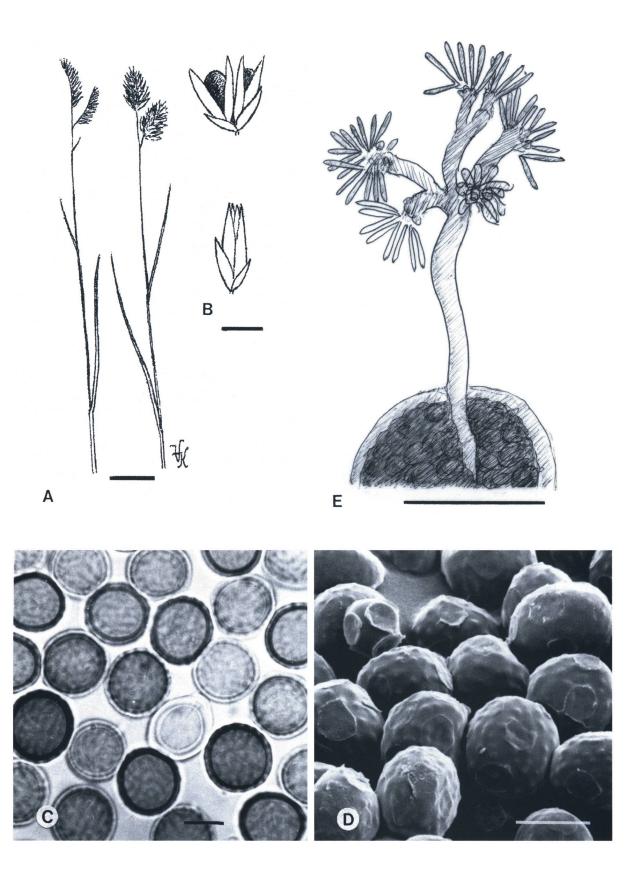
On Poaceae: Buchloë dactyloides (Nutt.) Engelm., Cathestecum erectum Vasey & Hack., C. procumbens Parl., C. prostratum Presl, Hilaria belangeri (Steud.) Nash, Muhlenbergia distichophylla (J. Presl) Kunth (Podosaemum distichophyllum J. Presl); N America (Mexico, USA).

Kellerman and Swingle (1889:12), and Chandra & Huff (2008) showed that infected male plants of the dioecious *Buchloë dactyloides* are transformed into female plants producing seeds filled with spores (transvestitism).

Ref.: Chandra & Huff 2008.

Fig. 74 A-D. *Salmacisia buchloëana* on *Buchloë dactyloides*, USA, Kansas, Newton, 15.VI.1939, leg. D. Cornelius, det. C.L. Lefebvre (as *Tilletia buchloëana*), HUV 14734.

- A. Sori in all ovaries of an infected inflorescence. Habit. Healthy inflorescence (left) (Bar = 1 cm).
- **B.** Enlarged a spikelet with two sori, and a healthy spikelet (Bar = 2 mm).
- C, D. Spores and sterile cells in LM and in SEM (Bars = $10 \mu m$).
- **E.** Spore germination (after Chandra & Huff 2008; Bar = $10 \mu m$).



75. *SCHIZONELLA* J. Schröter, in Cohn, *Beitr. Biol. Pfl.* 2:362, 1877.

Sori in leaves of Cyperaceae as black, short or long, pustulate streaks with agglutinated to powdery spore mass. Spores originally in pairs, arising by internal division of a mother cell, later may be separated into single spores. (In S. cocconii spores born in pairs are agglutinated into balls). Spore germination of Ustilago-type. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Type of the genus: S. melanogramma.

Schizonella, in the Anthracoideaceae, has five known species, one on Elyna, and four on Carex: 1. S. elynae (A. Blytt) Liro, 2. S. caricis-atratae Prillinger, Wuckowski & Lopandic, 3. S. cocconii (Morini) Liro, 4. S. intercedens Vánky & A. Nagler, and 5. S. melanogramma (DC.) J. Schröter. Because in S. cocconii the spores are agglutinated in more or less permanent spore balls, it was considered by some mycologists to be a member of the genus Tolyposporium. However, the type of sorus, the spore germination, and the fact that the spores are born in pairs, are typical Schizonella characters. The genus was merged with Schroeteria by Thirumalachar & Whitehead (1968), an unfortunate solution. The newly described S. caricis-atratae Prillinger, Wuczkowski & Lopandic, on Carex atrata, differs from S. melanogramma by its molecular phylogenetic characters only (= cryptic species).

Schizonella melanogramma (A.P. De Candolle) J. Schröter,

in Cohn, Beitr. Biol. Pfl. 2:385, 1877.

Uredo melanogramma De Candolle, Fl. franç., ed. 3, 6:75, 1815. — Caeoma melanogramma (DC.) Schlechtendal, Linnaea 1:238, 1826. — Puccinia melanogramma (DC.) Unger, Ueber den Einfluß des Bodens, etc.:217, 1836. — Thecaphora melanogramma (DC.) Léveillé, Ann. Sci. Nat. Bot., Sér. 3, 8:373, 1847. — Geminella melanogramma (DC.) Magnus, Hedwigia 14:19, 1875. — Lectotype (design. by Liro 1938:305) on Carex digitata L., France, Jura, leg. J.F. de Chaillet.

Ustilago destruens [subsp.] foliicola W. Hausmann, in Erb. Critt. Ital. no. 1300, 1865. — Geminella foliicola (Hausm.) J. Schröter, Abh. Schles. Ges. Vaterl. Cult. Abt. Naturwiss. 1869/72:6, 1869. — Type on Carex digitata, Italy, S Tirol, near Bolzano, 1860, Hausmann; isotypes in Erb. Critt. Ital. no. 1300, HUV 13855!

Ustilago ambiens P. Karsten, Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 29(2):108, 1872. — Entyloma ambiens (P. Karsten) Johanson, Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 41:160, 1884. — Type "in foliis graminum" (= Carex rupestris; comp. Liro 1938:307, and Lindeberg 1959:56), Spitsbergen, Advent Bay, 8.VIII.1868, Th.M. Fries, UPS!

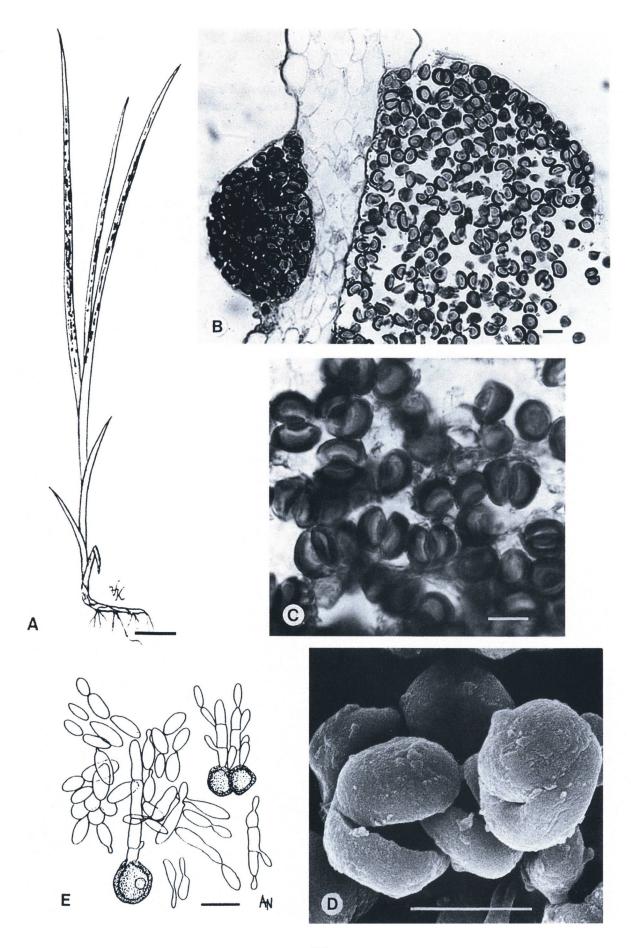
Urocystis pusilla Cooke & Peck, in Peck, Rep. (Annual) New York State Mus. Nat. Hist. 25:90, 1873. — Schizonella pusilla (Cooke & Peck) Ciferri, Ann. Mycol. 29:20, 1931. — Type on Carex pennsylvanica, USA, "Bethlehem and Center, May and June" (Syn. in Zundel 1953:50).

Sori (Figs. 75 A, B) in leaves and stems usually as epiphyllous, black, pustulate streaks of various length, initially intraepidermal, containing the semi-agglutinated, later almost powdery spore masses. Spores (Figs. 75 C, D) usually in pairs and connected at their median sides as a result of the partial division of the spore mother cell, subglobose, ovoid, usually irregularly hemispherical, 5-9(-10) x 8-13(-15) μm, olive-brown; spore wall smooth, rough to finely verruculose, usually thinner and lighter on the contact sides. Spore germination (Fig. 75 E) results in a 4-celled basidium of 3 + 1 arrangement, where the fourth cell remains included in the spore, the distal, three-celled part normally separates from the rest. Laterally and terminally the basidium develops ovoid to elongate basidiospores (Brefeld 1895:148-150, Pl. IX, figs. 6-12, Ingold 1992:166).

On Cyperaceae: on at least seventy-six *Carex* species; cosmopolitan.

Ref.: Brefeld 1895, Liro 1938, Vánky 1963, 1998a, Vánky & McKenzie 1990, Ingold 1992.

- **Fig. 75 A-D.** *Schizonella melanogramma* on *Carex digitata*, Hungary, Kaposvár, 5.VI.1963, S. Tóth, HUV 1524.
- **A.** Sori on the leaves. Habit (Bar = 1 cm). **B.** T.S. of a leaf with young, intraepidermal spores on one side of the leaf (left) and on the opposite side a mature sorus (right; Bar = 10 μ m). **C.** D. Spores in LM and in SEM (Bars = 10 μ m).
- E. Germination of spores from *Carex firma* Mygind ex Host (on WA, at room temp., in 2-3 days, after A. Nagler; Bar = $10 \mu m$).



76. *SHIVASIA* K. Vánky, M. Lutz & M. Piątek, in Lutz, Vánky & Piątek, *IMA FUNGUS* 3:147, 2012.

Sori in flowers of Cyperaceae (Schoenus) forming hard, globoid, black bodies composed of spore balls and spores on the surface of innermost floral organs developed in sporogenous hyphae in U-shaped pockets, at first covered by a fungal peridium. Spore balls few to many-spored, composed of spores only, no sterile cells. Spores pigmented (brown), without violet or reddish tint. Sterile cells absent.

Shivasia is currently a unispecific genus in the Anthracoideaceae within the order Ustilaginales. Molecular phylogenetic analyses showed that it is not related with the type of *Tolyposporium* and the other two species in that genus, and with any of the genera to which its type species was attributed. *Type of the genus*:

Shivasia solida (Berkeley) K. Vánky, M. Lutz & M. Piątek, in Lutz, Vánky & Piątek, *IMA FUNGUS 3*:147, 2012.

Ustilago solida Berk., in Hooker, Flora Tasmaniae 2:270, 1860. — Urocystis solida (Berk.) A. Fisch. Waldh., Aperçu Syst. Ustil.:38, 1877. — Sorosporium solidum (Berk.) McAlpine, Smuts of Australia:185, 1910. — Cintractia solida (Berk.) M. Piepenbr., Nova Hedwigia 70:310, 2000. — Tolyposporium solidum (Berk.) Vánky, Mycotaxon 110:320, 2009. — Type on Chaetospora (as 'Chaetophora') imberbis (= Schoenus apogon), Australia, Tasmania, Penquite, XII.1845, R.C. Gunn; isotype DAR 59818 (microscope slide).

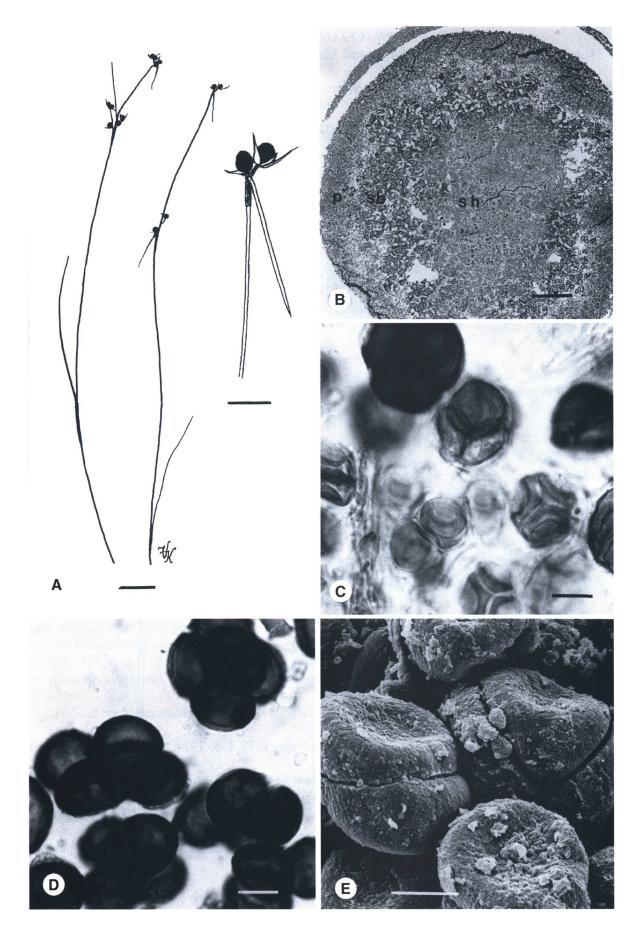
Sori (Figs. 76 A, B) in all flowers of an inflorescence, comprising the innermost floral organs, visible between the glumes as black, hard, globose to ovoid bodies, 1-2 mm in diameter, rarely also on the stems, then fusiform, at first covered by a thick, whitish brown fungal peridium of thick-walled, sterile hyphae that early flakes away exposing the compact mass of spore balls and spores, powdery on the surface. Spore balls (Figs. 76 D, E) usually irregular or globoid to ellipsoidal, composed of 2-15 spores, loose but rather permanent, 20-40 × 25-55(-70) μm, reddish brown. Spores (Figs. 76 D, E) subglobose, ovoid, elongate or irregular, flattened on one or two sides, 12-16 × 15-20 μm, yellowish to pale reddish brown; wall uneven, 0.5-1.5 μm thick, smooth to rough, in SEM finely, densely, irregularly verruculose and covered by remnants of the sporogenous hyphae. Spore balls and spores produced on the surface of host tissues in hyaline, sporogenous fungal tissues in radially arranged, U-shaped pockets (Fig. 76 C). Spore germiantion (on water, at room temp., in 3-5 days) results in long, aseptate basidia on which apically elongated, cylindrical basidiospores are produced. These germinate by filaments.

On Cyperaceae: Schoenus apogon Roem. & Schult. (S. brownii Hook. f.; Chaetospora imberbis R.Br.; S. imberbis R.Br.), S. calyptratus Kük., S. carsei Cheeseman, S. cruentus (Nees) Benth., S. latelaminatus Kük., S. maschalinus Roem. & Schult. (S. axillaris (R.Br.) Poir.), S. nanus (Lehm.) Benth., S. nitens (R.Br.) Hook. f. var. concinnus (Hook. f.) Cheeseman (S. concinnus Hook. f.), S. pauciflorus (Hook. f.) Hook. f., S. tesquorum J.M. Black, Schoenus sp.; Australasia (Australia, New Zealand).

Ref.: Lutz, Vánky & Piątek 2012

Fig. 76 A-E. *Shivasia solida* on *Schoenus apogon*, New Zealand, Auckland, Walkumete Cemetery, 26.X.1998, L.H.C. McKenzie, in Vánky, Ust. exs. no. 753, HUV 15059.

- **A.** Sori in all flowers of an inflorescence. Habit (Bars = 1 cm & 2 mm).
- **B.** T.S. of a sorus embedded in plastic, sectioned and stained with new fuchsin and crystal violet.
- $sh = sporogenous hyphae, sb = spore balls, p = peridium (Bar = 100 \mu m).$
- C. Spore ball formation in sporogenous fungal tissue on the surface of innermost floral organs (Bar = $10 \mu m$).
- **D, E.** Spore balls and spores in LM and in SEM (Bars = $10 \mu m$).



77. SPHACELOTHECA H.A. de Bary,

Verg. Morph. Biol. Pilze:187, 1884; emend. Langdon & Fullerton, Mycotaxon 6:421-456, 1978.

Sori in ovaries of plants in Polygonaceae, covered by a peridium. Peridium formed of host tissues and hyaline, catenate, non-sporogenous fungal cells, bursts at maturity. Columella present, formed of non-sporogenous fungal cells. Spores dark, violet-tinted, developed from hyphae at the base of the sorus, initially catenulate, connected by disjunctors, later solitary, with attached disjunctors. No sterile cells between the spores. Spore germination of Ustilago-type. Host-parasite interaction by intercellular hyphae lacking interactions, with deposits of specific fungal vesicles. Mature septa poreless.

Five species of *Sphacelotheca* are known, one on *Fagopyrum* and four on *Polygonum*: **1.** *S. fagopyri*, **2.** *S. hydropiperis*, **3.** *S. koordersiana*, **4.** *S. polygoni-serrulati*, and **5.** *S. serrulati-magna*. It belongs to the Microbotryaceae. The history, characterization and delimitation of this genus are discussed by Vánky & Oberwinkler (1994). *Type of the genus*:

Sphacelotheca hydropiperis (C.F. Schumacher) H.A. de Bary, **s. lat.**, *Verg. Morph. Biol. Pilze*:187, 1884.

Uredo hydropiperis Schumacher, Enumeratio Plantarum in partibus Saellandiae, etc., pars 2:234, 1803. — Ustilago hydropiperis (Schumach.) J. Schröter, in Cohn, Beitr. Biol. Pfl. 2:355, 1877. — Ustilago hydropiperis (Schumach.) Hirschhorn, Physis (Buenos Aires) 15:103, 1939 (comb. superfl.). — Ustilago hydropiperis (Schumach.) Ciferri, in Omagiu lui T. Săvulescu:166, 1959 (comb. superfl.). — Type on Polygonum hydropiper L., Denmark, Sjælland.

For taxonomic synonyms, such as *Caeoma utriculosum* Nees, *Ustilago polygoni-senticosi* Henn., *Sphacelotheca granosa* Liro, *S. excelsa* H. Sydow, *S. polygoni-filiformis* S. Ito, and *S. borealis* (G.P. Clinton) Schellenb. var. *chinensis* Zundel, see Vánky, *Smut Fungi of the World*, 2011('2012'):501-502.

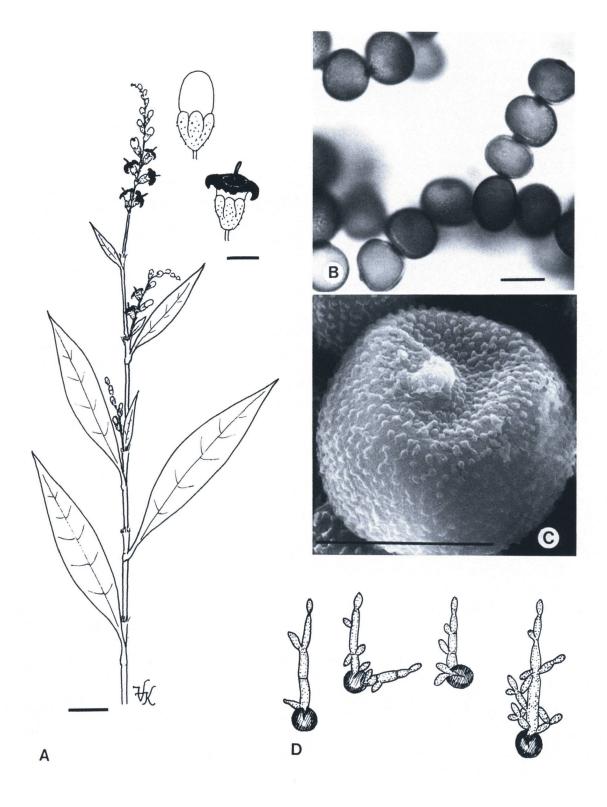
Sori (Fig. 77 A) in swollen ovaries as ovoid to cylindrical, 2-5 mm long bodies, initially covered by a grayish brown peridium, composed of pericarp tissues and fungal cells, bursting irregularly from the apex to expose the purplish black, powdery spore mass and a central columella. Columella composed mainly of fungal cells but includes host tissue remnants at the base. Infection systemic. *Spores* (Figs. 77 B, C) subglobose, ovoid to slightly irregular or slightly flattened, 9-13 x 10-15 μm, violet-tinted pale to medium reddish brown, minutely, abundantly verruculose, the warts just affecting the spore profile. The spores are formed in chains from the base of the sorus, when young held together by "disjunctors", at maturity easily separated but retaining disjunctors as small, hyaline, oppositely situated appendages. Seen in SEM 2-3 warts are often fused. Seen in TEM the spore wall around the disjunctors is thinner and less homogeneous than elsewhere. The disjunctors have a compact structure similar to that of the verrucae from the spore surface (Deml *et al.* 1985:236, fig. 8; Piepenbring *et al.* 1998:208, fig. 23). *Sterile cells* of the peridium and the columella varying in shape and size, globose, ellipsoidal or irregular, 8-16 μm long, hyaline. *Spore germination* (Fig. 77 D) results in four-celled basidia with laterally and terminally produced sessile basidiospores (Brefeld 1895).

On Polygonaceae: on at least twenty-four *Polygonum* species, including *Persicaria* (mainly on Sect. *Persicaria*); cosmopolitan.

S. hydropiperis is a species complex characterized by variable spore ornamentation as seen in SEM.

Ref.: Brefeld 1895, Schellenberg 1907, Langdon & Fullerton 1978, Liro 1924, Vánky & Oberwinkler 1994.

- **Fig. 77 A-D.** *Sphacelotheca hydropiperis* on *Polygonum hydropiper* L. A-C. Romania, Braşov, 24.IX.1960, leg. K. Vánky, HUV 1922.
- A. Sori in the ovaries. Habit (Bar = 1 cm). Enlarged a young sorus with peridium, and a mature, opened sorus with a visible central columella (Bar = 2 mm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$). Note the catenation of the spores in the LM picture, and a "disjunctor" of a spore in the SEM picture.
- **D.** Spore germination (after Brefeld 1895, Pl. VIII).



78. SPORISORIUM C.G. Ehrenberg ex H.F. Link, s. str.

in Link, Linné's Species Plantarum, Ed. 4, 6(2):86, 1825,

emend. McTaggart & R.G. Shivas, in McTaggart et al., Persoonia 29:118, 2012c.

LINDQUISTIA Subramanian & Chandrashekar, Bol. Soc. Argent. Bot. 18:150, 1977. — Type: L. indica Subram. & Chandrash. (n.v.).

Sori in flowers or inflorescence of plants in Poaceae, covered by a peridium formed of interwoven hyphae overlain by host tissue. Columella present, cylindrical, stout, woody, branched or unbranched, composed of host tissues permeated by inter- and intra-cellular hyphae which produce spores and sterile cells. Sporogenous hyphae uncoiled. Spores at first somewhat agglutinated, later single, pulverulent, pigmented (brown, without orange-yellow or violet tint). Sterile cells single, in groups or chains, hyaline, intermixed with the spores, formed from non-sporogenous partitioning hyphae. Spore germination of Ustilago-type. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Morphology (Vánky 1994:197-223; 2002a:142), spore germination (Ingold, 1994:467) and molecular phylogenetic characters (Stoll *et al.* 2003, 2005) show that *Sporisorium* s. lat. is not a natural genus. Its limits towards *Ustilago* and *Macalpinomyces* are not clear, with numerous intermediate forms. McTaggart *et al.* (2012c), based on morphological characters, host plant classification and molecular biological characters, divided the complex into seven genera: *Anthracocystis, Langdonia, Macalpinomyces, Sporisorium* s. str., *Stollia, Triodiomyces* and *Ustilago*. About 206 species of *Sporisorium* are known. *Type of the genus:*

Sporisorium sorghi C.G. Ehrenberg ex J.H.F. Link, in Linné's Species Plantarum, Ed. 4, 6(2):86, 1825.

Sphacelotheca sorghi (Ehrenb. ex Link) G.P. Clinton, J. Mycol. 8:140, 1902. — Cintractia sorghi (Ehrenb. ex Link) Hirschhorn, Rev. Argent. Agron. 6:198, 1939. — Type on Sorghum vulgare Pers. (= S. bicolor (L.) Moench], Egypt, leg. C.G. Ehrenberg. Neotype (design. by Vánky 1990c:275) on Sorghum bicolor, Egypt, Cairo, VI.1876, leg. G. Schweinfurth, HUV 1672!; isoneotypes in Thümen, Mycoth. univ. 725 (as U. reiliana Kühn forma sorghi-cernui on Sorghum cernuum). Paraneotype on Sorghum bicolor, Romania, Transylvania, near Odorhei [Székelyudvarhely], alt. c. 480 m, 5.IX.1963, leg. K. Vánky, HUV 2027!; isoparaneotypes in Vánky, Ust. exs. no. 50 (as Sphacelotheca sorghi on Sorghum vulgare; For neotypifying see Vánky 1990c:275).

For taxonomic synonyms such as *Ustilago sorghicola* Speg., and *Tilletia sorghi-vulgaris* Tul. & C. Tul., both on *Sorghum bicolor*, see Vánky, *Smut Fungi of the World*, 2011('2012'):745.

Sori (Figs. 78 A, B) in spikelets as 3-10 mm long, ovoid or cylindrical, pale brown bodies protruding from the glumes, covered by a well-developed peridium of interwoven hyphae overlain by host tissue, which ruptures irregularly to expose the dark brown, powdery spore mass and the central columella composed of host tissues permeated by hyphae. The panicles may or may not be congested and stunted. *Spores* (Figs. 78 C, D) when mature single, globose, subglobose, ovoid to slightly irregular, 5.5-7 x 5.5-8(-8.5) μm, pale olive-brown, from apparently smooth to sparsely punctate or very finely verruculose. *Sterile cells* somewhat larger than the spores, in irregular groups or chains, hyaline, smooth. *Spore germination* (Fig. 78 E) results in four-celled basidia (the 4th, basal cell usually remains in the spore) producing lateral and apical basidiospores in nutrient media, or infection hyphae in water (Clinton 1897, Pl. 5, Ingold 1986:474, fig. 1).

On Poaceae: Sarga and Sorghum species; cosmopolitan.

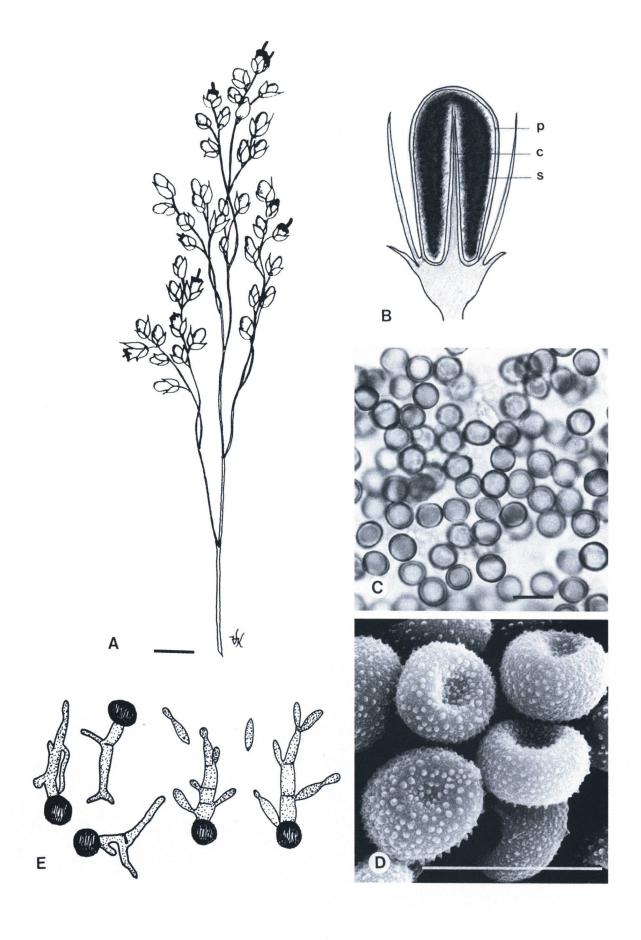
Report of *Cynodon dactylon* as host for this smut (Marley 1995) must be erroneous.

Ref.: Prillieaux 1895, Clinton 1897, Langdon & Fullerton 1975, 1978, Vánky 1990c, Ingold 1994, McTaggart, Shivas, Geering, Vánky & Scharaschkin 2012.

Fig. 78 A-D. *Sporisorium sorghi* on *Sorghum bicolor* (L.) Moench, paraneotype, Vánky, Ust. exs. no. 50 (as *Sphacelotheca sorghi*), HUV 2027. **A.** Part of a panicle with sori in the spikelets. Habit (Bar = 1 cm).

B. L.S. of a sorus, schematized. p = peridium, c = columella, s = spores and groups of sterile cells.

C, D. Spores in LM and in SEM (Bars = $10 \mu m$). E. Spore germination in water (left) and in nutrient media (right; Clinton 1897, Pl. V).



79. *STEGOCINTRACTIA* M. Piepenbring, D. Begerow & F. Oberwinkler, *Mycologia 91*:497, 1999.

Sori on plants in Juncaceae, in all spikelets or around pedunculi of an infected inflorescence forming a black, agglutinated spore mass with a powdery surface. Young sori covered by a fungal peridium, sterile stroma lacking. Infection systemic. Spores single, pigmented (brown), ornamented, without appendages. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Stegocintractia, in the Anthracoideaceae, is one of the three genera resulted from the splitting of Cintractia s. lat. (see also Leucocintractia and Ustanciosporium). It has six known species 1. S. capitata K. Vánky, H. Jage, U. Schlüter & H. Sluschny on Juncus capitatus Weigel, 2. S. hyperborea (A. Blytt) M. Piepenbr. on Luzula species, 3. S. junci (Schwein.) M. Piepenbr. on Juncus species, 4. S. lidii (Liro) M. Piepenbr. on Juncus biglumis L., 5. S. spadicea (Liro) M. Piepenbr. & Begerow on Luzula alpinopilosa (Chaix) Breistr., and 6. The type of the genus:

Stegocintractia luzulae (P.A. Saccardo) M. Piepenbring, D. Begerow & F. Oberwinkler, Mycologia, 91:497, 1999.

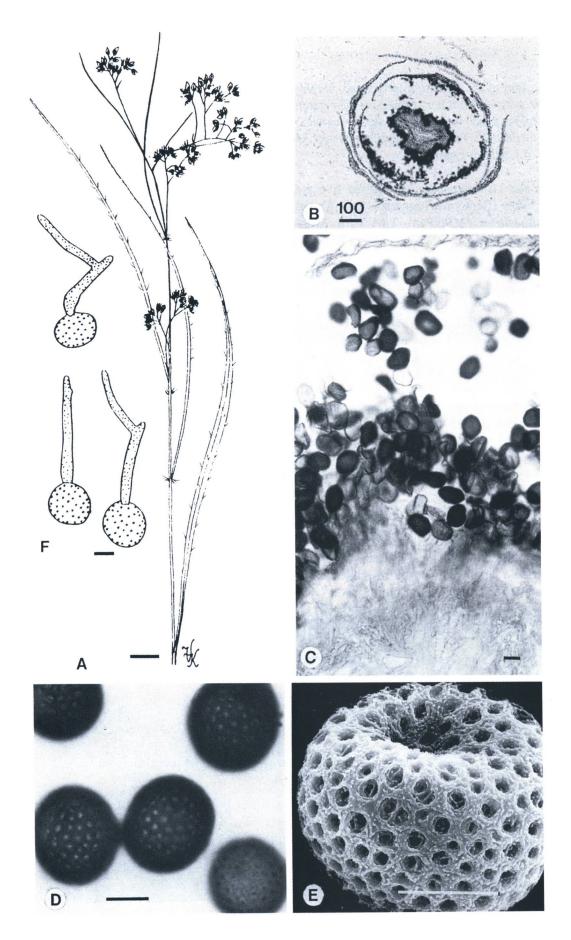
Ustilago luzulae Saccardo, Atti Soc. Veneto-Trentina Sci. Nat. (Padova) 2:121, 1873. — Cintractia luzulae (Sacc.) G.P. Clinton, J. Mycol. 8:143, 1902. — Type on Luzula forsteri, Italy, "in sylva Cansiglio, agri Tarvisini", leg. G.A. de Bérenger.

Sori (Figs. 79 A, B. C) in all the spikelets of an inflorescence surrounding the basal part of the glumes and the axis of the sterile spikelets, spherical to ovoid, c. 1 x 1.5(-2) mm, composed of a black, initially agglutinated, later more or less powdery spore mass covered by an inconspicuous peridium and hidden by the glumes. Infection systemic. Spores develop in a hyaline matrix on the surface of the host tissues, without sterile stroma. Spores (Figs. 79 D, E) single, slightly flattened, in side view 18-20 μm wide, in plane view circular, ovate to irregular, 19-24(-26) x 20-30(-32) μm, dark reddish brown with pale spots; wall c. 2 μm thick, finely and densely foveolate to reticulate, in SEM deeply foveolate with verrucose surface. Spore germination (Fig. 79 F) results in ramified hyphae (Piepenbring, 2000).

On Juncaceae: Luzula campestris (L.) DC., L. forsteri (Sm.) DC., L. luzulina (Vill.) Dalla Torre & Sarnth., (L. flavescens (Host) P. Beauv.) Gaudin), L. luzuloides (Lam.) Dandy & Wilmott, (L. nemorosa (Pollich) E. Mey.; L. albida (Hoffm.) DC.), L. multiflora (Retz.) Lej., L. multiflora subsp. frigida (Buchenau) V. Krecz. (L. frigida (Buchenau) Sam.), L. nivea (L.) DC., L. pilosa (L.) Willd. (L. vernalis (Reichard) DC.), L. sieberi Tausch, L. spicata (L.) DC., L. sudetica (Willd.) DC., L. sylvatica (Hudson) Gaudin (L. maxima DC.), L. wahlenbergii Rupr.; Europe, E Asia, N America.

Ref.: Clinton 1904, Schellenberg 1911, Liro 1938, Piepenbring, Begerow & Oberwinkler 1999, Piepenbring 2000.

- Fig. 79 A-E. Stegocintractia luzulae on Luzula pilosa, Vánky, Ust. exs. no. 60 (as Ustilago luzulae), HUV 4056
- A. Sori in all spikelets of an inflorescence. Habit (Bar = 1 cm).
- **B**, C. T.S. of a sorus with spores developed on the surface of the host plant.
- **D**, **E**. Spores in LM and in SEM (Bars = $10 \mu m$).
- F. Spore germination (on WA, at room temp., in 3 days; after Piepenbring, 2000:325).



80. STOLLIA A.R. McTaggart & R.G. Shivas,

in McTaggart, Shivas, Geering, Vánky & Scharaschkin, Persoonia 29:128, 2012c.

Sori in swollen ovaries of Andropogoneae, localized in the inflorescence, globose to obovoid, covered by a thick peridium derived from host tissue, initially green, darker with age, which ruptures at maturity to expose the pulverulent spore mass mixed with sterile cells. Spores single, globose, subglobose to ellipsoidal, often echinulate. Sterile cells in loose irregular groups, globose, hyaline. Columellae and spore balls are lacking. Germination of Ustilago-type.

Stollia, in the Ustilaginaceae, comprises five species: 1. S. bothriochloae (L. Ling) McTaggart & R.G. Shivas, 2. S. bursa (Berk.) McTaggart & R.G. Shivas, 3. S. ovariicolopsis (Vánky) McTaggart & R.G. Shivas, 4. S. pseudanthestiriae (A.R. Patil, T.M. Patil, M.S. Patil) McTaggart & R.G. Shivas, and 5. The type of the genus:

Stollia ewartii (D. McAlpine) A.R. McTaggart & R.G. Shivas, in McTaggart, Shivas, Geering, Vánky & Scharaschkin, *Persoonia* 29:128, 2012c.

Ustilago ewartii McAlpine, Proc. Linn. Soc. New South Wales 36:45, 1912('1911'; as 'ewarti'). — Macalpinomyces ewartii (McAlpine) K. Vánky & R.G. Shivas, Mycotaxon 80:346, 2001. — Type on Sorghum stipoideum (= Sarga timorense), Australia, Western Australia, Napier, Broome Bay, 22.V.1910, A.J. Ewart, VPRI 3099; MEL 1055129.

Ustilago sorghi-stipoidei L. Ling, Sydowia 7:154, 1953. — Type on Sorghum stipoideum (= Sarga timorense), Australia, Northern Territory, Katherine, 24.IV.1947, S.T. Blake, MEL 1055129; isotypes BPI 166531, BRIP 7791, IMI 43753, HUV 17928! (Syn. by Vánky 1997:153).

Sori (Fig. 80 A) in considerably swollen ovaries, only a few in each inflorescence infected, obovoid with a tapering basal part and a shortly acute tip, with remnants of the styles, more rarely lemon-shaped, 4-10 \times 8-15 mm, covered by a thick, initially green, later brown peridium that ruptures at maturity exposing the brown, powdery mass of spores mixed with groups of sterile cells. *Spores* (Figs. 80 B, C) globose, subglobose or ellipsoidal, variable in size, 9-14.5 \times 9-15 μ m, yellowish brown; wall uniformly thick, with dense conical spines, 0.5-1.5 μ m high and 0.5-1 μ m wide at their base. *Sterile cells* (Figs. 80 B, C) in large, loose, irregular groups; individual cells globose, ovoid, ellipsoidal to slightly irregular, 8-13 \times 8-16 μ m, hyaline, contents homogeneous; wall uniformly 0.5-0.8 μ m thick, smooth. *Spore germination* (McAlpine 1912('1911'):46) results in septate basidia of variable length, composed of numerous cells producing lateral and terminal 3-6 μ m long, fusiform basidiospores often in chains of 3 or more.

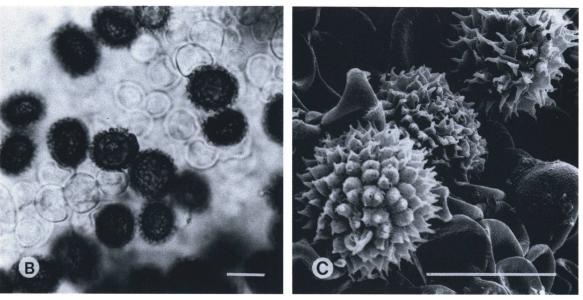
On Poaceae: Sarga intrans (F. Muell. ex Benth.) Spangler (Sorghum intrans F. Muell. ex Benth.), Sa. plumosa (R.Br.) Spangler (So. plumosum (R.Br.) P. Beauv.; So. interjectum Lazarides), Sa. timorense (Kunth) Spangler (So. timorense (Kunth) Büse; Sa. stipoidea Ewart & Jean White; So. stipoideum (Ewart & Jean White) C.A. Gardner & C.E. Hubb.), Sorghum nitidum (Vahl) Pers.; SE Asia (Thailand), Australia.

Ref.: McTaggart, Shivas, Geering, Vánky & Scharaschkin 2013.

Fig. 80. Stollia ewartii on Sarga timorense (Sorghum timorense, So. stipoideumn), Vánky, Ust. exs. no. 1094, HUV 19412.

- **A.** Sori in some ovaries. Habit, and enlarged a sorus and a healthy spikelet pair (Bars = 1 cm).
- **B, C.** Spores and sterile cells in LM and in SEM (Bars = $10 \mu m$).





81. *TALBOTIOMYCES* K. Vánky, R. Bauer, D. Begerow, *Mycol. Balcan.* 4:12, 2007.

Sori on roots of dicotyledonous host plants producing galls. *Spores* intracellular, ornamented, subhyaline, weakly pigmented (lacking brown, black, reddish or violet color). *Septal pore* simple. *Host-parasite interaction* by haustoria.

Talbotiomyces is a unispecific genus belonging probably to the Entorrhizomycetes. Type of the genus:

Talbotiomyces calosporus (P.H.B. Talbot) K. Vánky, R. Bauer & D. Begerow, *Mycol. Balcan.* 4:12, 2007.

Entorrhiza calospora P.H.B. Talbot, Bothalia 6:453, 1956. — Type on Limeum glomeratum (= L. viscosum subsp. viscosum var. glomeratum), South Africa, Transvaal, Pretoria, Brummeria, near Murray Farm, 30.I.1943, leg. J.J.O. Pazzi, PREM 33770; isotype HUV 587! Topotype: spring 1944, leg. J.J.O. Pazzi, PREM 35291, 35391. Paratypes on Limeum viscosum, Transvaal, Pretoria, near Brummeria, Pretoria University Farm, Botanical Reserve, leg. P.H.B. Talbot, PREM; on Limeum viscosum, Orange Free State, Ficksburg, III.1955, leg. Dr. Meredith, PREM 41034; on Trianthema pentandra, Orange Free State, near Malaty, 8.IV.1945, leg. B.N. Wolff, PREM 39031.

Sori (Fig. 81 A) on roots forming galls, from 0.5 mm to 3.5 cm in diameter, initially smooth, later rough, tubercular, globoid, irregular or elongate and fused, surrounding the root or situated on its side, then asymmetrical, pale yellowish brown, compact, composed of vascular bundles and parenchymatous cells with fungal mycelium, haustoria and intracellularly developed spores, up to twenty per host cell. Spore mass lemonto golden-yellow, agglutinated, not powdery. *Spores* (Figs. 81 B, C) globose, subglobose to ellipsoidal, varying in size, $14-21.5 \times 16-25 \mu m$ (including ornamentation), subhyaline to pale yellow; endospore even, $0.5-0.8 \mu m$ thick, exospore ornamented with moderately densely situated cylindrical warts, $1.5-2.5(-3.5) \times 1.5-4 \mu m$. Warts on the same spore varying in length and width, from short, nearly subpyramidal to long-cylindrical with a rounded tip; (4-)5-9 warts per spore diameter, 12-22 on the spore circumference. *Spore germination* unknown.

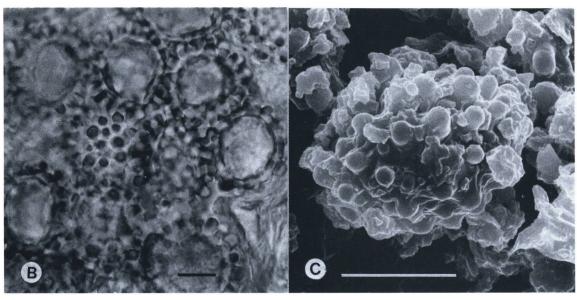
On Molluginaceae: Limeum viscosum (J. Gay) Fenzl, L. viscosum subsp. viscosum var. glomeratum (Eckl. & Zeyh.) Friedrich (L. glomeratum (J. Gay) Eckl. & Zeyh); On Aizoaceae: Trianthema pentandra L.; On Portulacaceae: Portulaca oleracea L.; South Africa.

Ref.: Talbot 1956, Vánky, Bauer, Begerow 2007.

Fig. 81 A-C. Talbotiomyces calosporus on Limeum viscosum, isotype, HUV 587.

- **A.** Sori on roots forming globoid galls on an apparently healthy plant (Bar = 1 cm).
- B, C. Spores in LM (in lactophenol with cotton blue) and in SEM.





82. TESTICULARIA J.F. Klotzsch,

Linnaea 7:202, 1832.

MILLERIA Peck, Annual Rep. New York State Mus. 31:40, 1879, not Milleria Linnaeus, 1753. — Type: M. herbatica Peck on Rhynchospora macrostachya, USA, New York, Wading River, E.S. Miller, in Ellis, N. Amer. fgi. no. 805.

Sori in spikelets of host plants in Cyperaceae (*Rhynchospora*) forming sac-like swellings, covered by a thick peridium, filled with a black, agglutinated or granular mass of spore balls. Between the young spore balls fascicles of long, sterile, fungal cells are present, arranged more or less radially. *Spore balls* many-spored, composed of an external layer of darkly pigmented (brown) spores and a central mass of sterile cells. *Spore germination* results in phragmobasidia. *Host-parasite interaction* by intracellular hyphae, coated by an electron-opaque matrix. Mature *septa* poreless.

Tentatively, *Testicularia* is placed in the Anthracoideaceae, it has three known species, all on *Rhynchospora*: 1. *T. africana* Vánky & Piątek, 2. *T. minor* (Juel) L. Ling, and 3. The *type of the genus*:

Testicularia cyperi J.F. Klotzsch,

Linnaea 7:202, 1832.

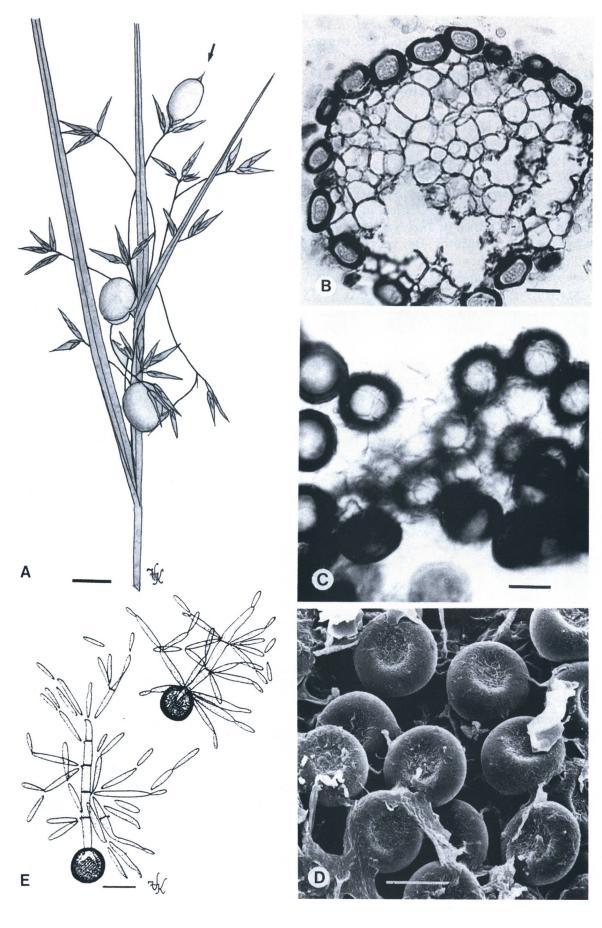
Type on *Rhynchospora* sp., N America (no closer data), herb. Hooker, K (n.v.); isotype BPI 711939 (n.v.). *Milleria herbatica* Peck, *Annual Rep. New York State Mus. 31*:40, 1879. — Type on *Rhynchospora macrostachya*, USA, New York, Wading River, no date, leg. E.S. Miller; isotypes in Ellis, N. Amer. fgi. no. 805, HUV 2039!

Sori (Fig. 82 A) comprise some spikelets of an inflorescence, forming conspicuous, subglobose, ellipsoidal or ovoid swellings, 5-20 mm long, covered by a thick, whitish peridium. This is composed of hyaline, subglobose, ellipsoidal, elongate or irregular, firmly united fungal cells, 7-16 × 8-25 μm; wall varying in thickness, 1.5-6.5 μm wide, often with gelatinized external layer. At maturity, the peridium ruptures irregularly at the apex, becoming sac-like, and the black, agglutinated or granular-powdery mass of spore balls is exposed. The sori comprise all flowers of a spikelet, leaving intact the basal glumes and rarely also the tip of the distal floral envelopes (Fig. 82 A, arrow). In some sori there is a well-developed, irregular columella, the axis of the spikelet. In young sori, between the spore balls, more or less radially arranged sterile hyphae can be seen. Spore balls (Fig. 82 B) subglobose, ovoid to irregular, (60-)70-200-260) × 75-320(-350) μm, dark chestnut-brown, opaque, composed of an external, often incomplete layer of spores and an internal mass of sterile, parenchymatous cells. Spores (Figs. 82 B, C, D) tangentially slightly flattened, in side view elliptic or slightly irregular, 9-13.5 µm wide, in plane view circular or subcircular, 13-16(-17) µm in diameter, reddish- to chestnut-brown; wall uneven, 1-3 µm, thinner on the flattened, outer surface, smooth, in SEM finely, densely granular-verruculose. Spore germination (Fig. 82 E) results in phragmobasidia measuring 3-4 × 30-45 µm, composed of 3-6 cells. On the basidia, on sterigmata, laterally and terminally, narrowly ellipsoidal to subfusiform basidiospores are produced measuring (1.5-)2-3 × 8-16 μm. Basidiospores one- or two-celled, germinating by similar but smaller secondary and tertiary spores often on sterigmata, and also producing yeast colonies in nutrient media. Sterile cells (Figs. 82 B, C) irregularly polyhedral, 5-12 × 6-13.5 μm, thin-walled (c. 0.3 μm), yellowish to brownish tinted, smooth.

On Cyperaceae: *Rhynchospora careyana* Fernald, *R. corniculata* (Lam.) A. Gray (*R. laxa* Vahl), *R. macrostachya* Torr. ex A. Gray; North America (USA).

Ref.: Klotzsch 1832, Juel 1897, Ling 1951b, Whitehead & Thirumalachar 1969, Vánky & Piatek 2006.

Fig. 82 A-D. Testicularia cyperi on Rhynchospora macrostachya. Type of Milleria herbatica Peck, Ellis, N. Amer. fgi. no. 805, HUV 2039. A. Sori in scattered spikelets. Habit. One sorus with remnants of floral envelopes (arrow; Bar = 1 cm). B. T.S. of a spore ball with dark, thick-walled spores on the surface of a mass of empty, sterile, parenchymatous cells (Bar = $10 \mu m$). C. Spores and fragments of sterile cells in a squashed spore ball in LM, and D. Spores on the surface of a spore ball in SEM (Bars = $10 \mu m$). E. Germinating spores of T. cyperi on Rhynchospora careyana, Vánky, Ust. exs. no. 1032, HUV 18603 (on MYP, at room temp., in 3 days, R. Bauer; Bar = $10 \mu m$).



83. THECAPHORA C.A. Fingerhuth, nom. cons.

Linnaea 10:230, 1836; emend. Vánky, Mycotaxon 69:94, 1998.

SOROSPORIUM F. Rudolphi, *Linnaea* 4:116, I.1829, nom. rej. (ICBN/Vienna, 2006:223). — Type: *S. saponariae* F. Rudolphi, *Linnaea* 4:116, 1829 (= *Thecaphora saponariae* (F. Rudolphi) Vánky), on *Saponaria officinalis* L., Germany.

POIKILOSPORIUM Dietel, Flora 83:87, 1897. — Type: P. davidsohnii (Dietel & Holway) Dietel (= Thecaphora piluliformis Berk. & Curtis, as "pilulaeformis"), on "Atriplex sp." (= Bigelowia veneta A. Gray, det. Clinton 1902:145), USA.

GLOMOSPORIUM Kochman, Acta Soc. Bot. Poloniae 16:58, 1939. — Type: G. leptideum (H. Sydow) Kochman. (= Thecaphora leptideum (H. Sydow) Zundel). (Syn. by Vánky, Lutz & Bauer 2008a:37).

ANGIOSORUS Thirum. & M.J. O'Brien, in O'Brien & Thirum., Sydowia 26:201, 1974('1972'). — Type: A. solani Thirum. & M.J. O'Brien (= Thecaphora solani (Thirum. & O'Brien) Mordue), on Solanum tuberosum L. subsp. andigenum (Juz. & Bukasov) Hawkes, Venezuela. (Syn. by Mordue 1988:177, and Vánky 1988:370).

TOTHIELLA Vánky, Mycotaxon 70:39, 1999. — Type: T. thlaspeos (Beck) Vánky. (= Thecaphora thlaspeos (Beck) Vánky, on Thlaspi alpestre L., Austria. (Syn. by Vánky 2004d:110).

KOCHMANIA Piątek, Mycotaxon 92:34, 2005. — Type: K. oxalidis (Ellis & Tracy) Piątek. (= Thecaphora oxalidis (Ellis & Tracy) M. Lutz, R. Bauer & Piątek., on Oxalis stricta, USA. (Syn. by Vánky et al. 2008a:37).

Sori in various parts of dicotyledonous host plants, filled with masses of spore balls, rarely spores single, yellowish- to dark reddish brown, never black, and without a violet tint. Peridium and columella lacking. Spore balls composed of few to many, loosely or firmly agglutinated spores only. Spores subpolyhedrally irregular, often wedge-shaped, more rarely globose or broadly ellipsoidal; wall thin, smooth or nearly so on the contact sides, thick and ornamented on the free side. In some cases the whole surface is ornamented, exceptionally the spores are smooth. Spore germination not uniform, typically results in germ tubes, often with a basal swelling (basidia?), initially aseptate, later septate, with or without ramifications and conjugations, growing out as filaments producing apically or subapically ovoid or cylindrical, aerial "sporidia", often on terminal ramifications. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Lectotype (design. by Clements & Shear 1931:339): T. hyalina Fingerh. (= T. seminis-convolv.).

Thecaphora, in the Glomosporiaceae, has 61 species on members of 16 dicotyledonous host plant families.

Thecaphora seminis-convolvuli (J.B.H.J. Desmazières.) S. Ito,

Trans. Sapporo Nat. Hist. Soc. 14:94, 1935.

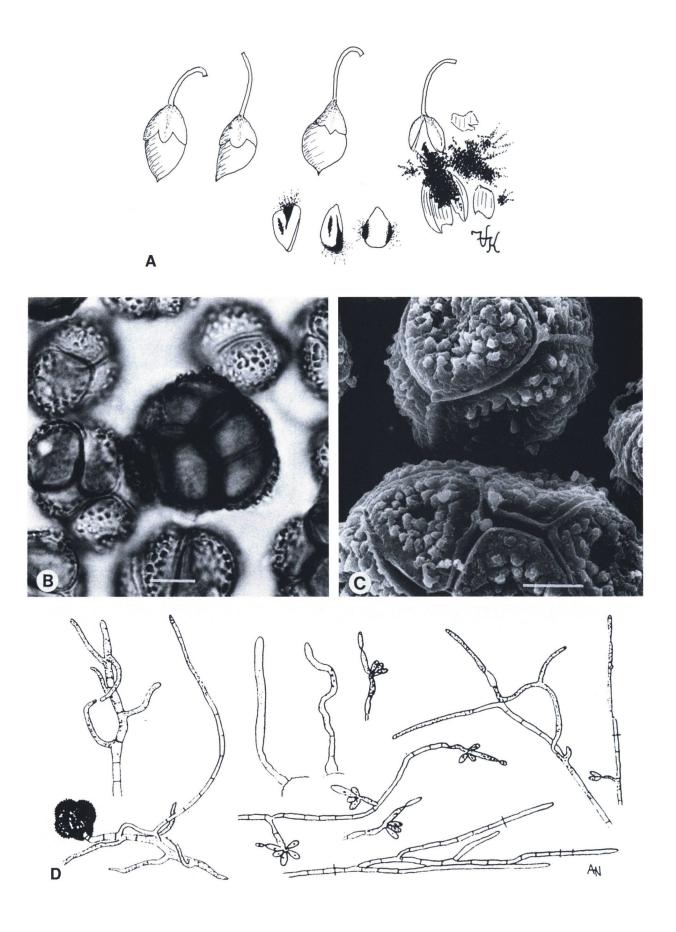
For nomenclatural and taxonomic synonyms such as: *Uredo seminis-convolvuli* Desm., *Ustilago capsularum* Fr., *Thecaphora capsularum* (Fr.) Magnus, *Thec. convolvuli* Rostr., *Tuburcinia convolvuli* ("Desm.") Rostr., and *Thec. hyalina* Fingerh., and *Thec. convolvuli* Schilb., see Vánky, *Smut Fungi of the World*, 2011('2012'):839.

Sori (Fig. 83 A) destroying partly or totally one or more seeds in scattered capsules, filling the capsules with a granular-powdery, reddish brown spore mass. Spore balls (Figs. 83 B, C) persistent, globose, ovoid to irregular, 20-55 μm long, composed of 2-10(-18?) spores. Spores (Figs. 83 B, C) hemispherical, wedge-shaped, subpolyhedral to irregular, 11-16 x (13-)15-24(-35) μm, palw reddish brown; wall smooth on the contact sides, coarsely and densely verrucose to echinulate on the free surface, warts up to 2.5 μm high. Spore germination (Fig. 83 D) results in a septate basidium with thin branches, some of which fuse in pairs to produce hyphae. At the end of hyphal branches one to several ovoid or long ellipsoidal "conidia" are produced (Woronin 1882('1881'):577, Pl. III, figs. 19-28, Nagler 1986:56-60, figs. 26-27). Anamorph (Thecaphorella antherarum (Oudemans) H. & I. Scholz) is produced in the anthers.

On Convolvulaceae: Calystegia sepium (L.) R.Br. (Convolvulus sepium L.), and its var. japonicus Mak., Ca. soldanella (L.) R.Br. (Convolvulus soldanella L.), Convolvulus arvensis L.; Europe, Asia, N America.

Ref.: Liro 1938, Mayor 1949, Henderson 1956, Carranza & Lindquist 1962, Brett 1966, Zambettakis & Joly 1975, Durán 1982, Nagler 1986, Vánky & Berbee 1988, Vánky 1991b, 1998a, 1998b, Vánky, Lutz & Bauer 2008a.

Fig. 83 A-D. *Thecaphora seminis-convolvuli* on *Convolvulus arvensis*. A-C. Vánky, Ust. exs. no. 3, HUV 2114. A. Sori in the seeds. Habit. B, C. Spores and spore balls in LM and in SEM (Bars = $10 \mu m$). D. Spore germination (after Woronin, 1882('1881'), Pl. III, and after Nagler, 1986:60).



84. *TILLETIA* Tul. & C. Tulasne, *Ann. Sci. Nat. Bot.*, *Sér. 3*, 7:112, 1847.

Sori on host plants in Poaceae, most commonly in the ovaries, forming "bunt balls" filled with semi-agglutinated to powdery, pale to dark brown spore masses, intermixed with sterile cells. Sori sometimes also as streaks on leaves and culms, rarely producing swellings or witches' brooms, exceptionally as cover on the surface of leaves, often fetid from trimethylamine (odor of herring brine). Peridium and columella lacking. Infection systemic or local. Spores single, medium to large sized, usually ornamented: reticulate, cerebriform, verrucose, spiny, tuberculate or with cylindrical warts ("projections"), rarely smooth, often encased in a hyaline gelatinous sheath. Sterile cells usually present between the spores, solitary, variously shaped, smooth but also weakly or evidently ornamented (called also "immature spores"), hyaline or slightly pigmented, naked or sheathed. Spore germination by means of an aseptate basidium (holobasidium), bearing terminal basidiospores which often conjugate in situ, giving rise to infection hyphae, blastospores and ballistospores (secondary sporidia), or basidiospores numerous, acicular, giving rise to infection hyphae without conjugation. Host-parasite interaction by intercellular hyphae; interaction apparatus is lacking. Septal pore is a dolipore traversed by two membranous plates, pore caps lacking. Type of the genus: T. caries.

Tilletia, the type of the Tilletiaceae, has about 180 known species, parasitizing members of Poaceae. Several Tilletia species were considered to be Neovossia by different mycologists, based on characters such as the great number of acicular, non-conjugating basidiospores. Having similar septal pore structure (see above), Tilletia is closely related to Conidiosporomyces, Ingoldiomyces, Neovossia and Oberwinkleria (but not to Erratomyces). The relationship was confirmed also by DNA analyses. Therefore, and not taking into consideration morphological characters, a few or all of these genera were merged with Tilletia by some recent mycologists. Tilletia was revised by Massee (1899), and treated by Durán & Fischer (1961), using numerical taxonomy.

Tilletia caries (A.P. De Candolle) Tul. & C. Tulasne, *Ann. Sci. Nat. Bot.*, *Sér. 3*, 7:113, 1847.

Uredo caries De Candolle, Fl. franç., ed. 3, 6:78, 1815. — Type on "froment" (= Triticum aestivum), France. Lycoperdon tritici Bjerkander, Kongl. Vetensk. Acad. Handl. 36:326, 1775 (nom. nud.). — Tilletia tritici (Bjerk.) R. Wolff, Der Brand des Getreides, etc.:13, 1874 (n.v.). — Tilletia tritici (Bjerk.) G. Winter, Rabenh. Krypt.-Fl., 2 Aufl., 1(1):110, 1881. — On Triticum aestivum.

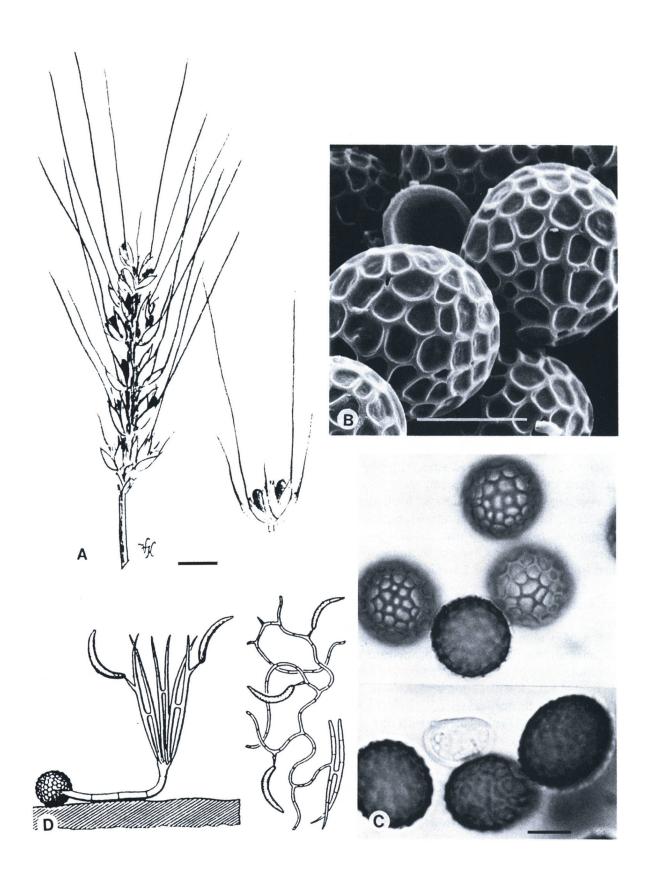
Uredo sitophila Ditmar, in Sturm, Deutschlands Flora, Abt. III, Heft 3, Die Pilze Deutschlands, Nürnberg:69,
1816. — Caeoma sitophilum (Ditmar) Link, in Linné's Species Plantarum, Ed. 4, 6(2):2, 1825. — Tilletia sitophila (Ditmar) J. Schröter, in Cohn, Beitr. Biol. Pfl. 2(3):365, 1877. — Type on "Weizen" (= Triticum aestivum), Germany.

Sori (Fig. 84 A) filling the ovaries with a reddish brown to dark brown, semi-agglutinated to pulverulent, fetid spore mass. Spores (Figs. 84 B, C) globose to subglobose, (14-)16-20(-25) μm in diameter, pale yellow to reddish brown; wall reticulate, 5-8 meshes per spore diameter, meshes 2.5-6 μm wide, muri 0.5-1.5 μm high, 19-28 on the spore circumference. Sterile cells (Figs. 84 B, C) globose to subglobose, 10-18 μm in diameter, hyaline to subhyaline, smooth, thin-walled (0.5-1.5 μm). Hyphae mostly intercellular (Luttrell 1987:2582, figs. 1-3). Spore germination (Fig. 84 D) results in aseptate basidium on which 8-16, elongate basidiospores are produced apically. These fuse to produce dikaryotic hyphae which may directly infect host seedling coleoptiles or produce further ballistospores.

On Poaceae: Aegilops, Agropyron, Amblyopyrum Arrhenatherum, Elymus, Secale, Sitanion, Triticum species, artificially also on Alopecurus, Bromus, Dactylis, Festuca, Hordeum, Koeleria, Lolium species; cosmopolitan.

Ref.: Massee 1899, Liro 1938, Mundkur 1944b, Hulea 1947, Holton & Kendrick 1956, Fischer 1956, Durán 1957, Nieman 1957, Durán & Fischer 1961, Hirschhorn & Calvo 1963, Zogg 1972, 1983, Ingold 1987b.

Fig. 84 A-D. *Tilletia caries* on *Triticum*. A. Sori in ovaries of *Triticum aestivum* L. B, C. Spores and sterile cells in LM and in SEM from *Triticum monococcum* L., Herb. myc. rom. no. 535, HUV 2198. D. Spore germination (after Buller & Vanterpool 1925:934).



85. *TILLETIARIA* R.J. Bandoni & B.N. Johri, *Canad. J. Bot. 50*:39, 1972.

A curious fungus which produced teliospores that germinated giving rise to septate basidia producing ballistosporic basidiospores on sterigmata was isolated from decayed wood by Bandoni & Johri (1972). It was described as a new species and genus (and later also a new family, Tilletiariaceae R.T. Moore).

Tilletiaria, currently a unispecific genus, is characterized by uninucleate, hyaline, branched, septate hyphae that bear both teliospores and ballistospores. Ballistospores formed on scattered sterigmata. Teliospores terminal or intercalarly, brown. The metabasidia are cylindrical, transversely septate, as in the Ustilaginaceae, but ballisto-basidiospores are produced on their sterigmata. Basidiospores germinate by germ tube or by repetition. The delicate, branched mycelium bearing narrow, arcuate ballistospores resembles that of some *Tilletia* and *Tilletiopsis* species. *Type of the genus:*

Tilletiaria anomala R.J. Bandoni & B.N. Johri,

Canad. J. Bot. 50:40, 1972.

Habitat: Superficial, on decayed wood, with *Poria* sp., VIII.1967, Canada, British Columbia, Vancouver. — Holotype: U.B.C. Culture no. 951, American Type Culture Collection, Manassas, Virginia, USA.

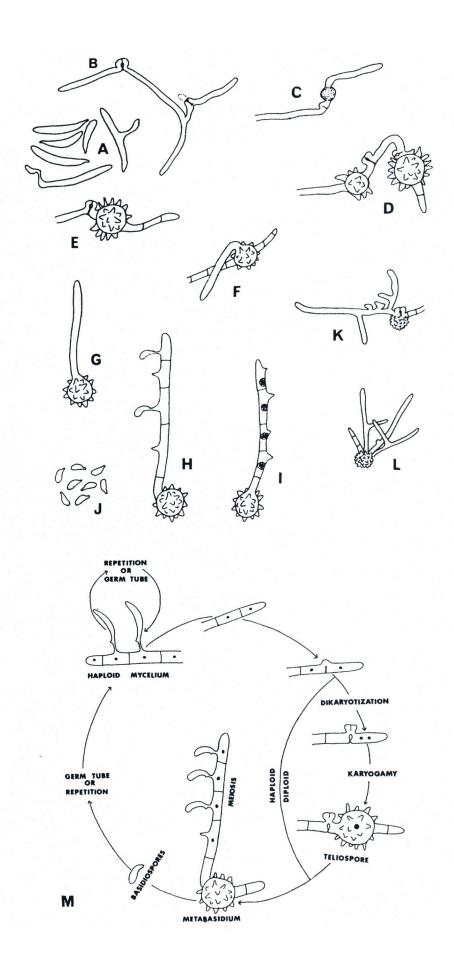
Colonies on MYP at first buff, slightly raised, becoming fawn colored to vinaceous brown or warm blackish brown (Ridgway 1912), typically with a pale-colored, centrally raised area and a darker zone outward, the margin remaining pallid; colonies compact, the surface often convoluted and buckling. *Hyphae* (Fig. 85 B) hyaline, with numerous simple septa, branched, 2-4.5 μm in diameter, bearing teliospores and ballistospores. *Ballistospores* (Fig. 85 A) formed on scattered or sometimes clustered sterigmata, subfusiform, curved, tapering slightly distally, abruptly narrowed basally, 2.5-5 x 6.5-16(-20) μm, germinating by germ tube or by repetition. *Teliospores* (Figs. 85 C-I) formed singly within short branches or, less frequently, intercalarly or in pairs, the short branches usually with a clamp-like structure adjacent to the teliospore, spores brown, aculeate for the most part but some tuberculate or almost smooth, globose or subglobose, 7.5-12.5 μm in diameter (excluding spines); aculeae conical, mostly blunt, 2-3 μm wide basally and up to 4 μm high; terminal teliospores each with a terminal appendage, the latter cylindrical, hyaline, zero- to three-septate, 2.5-3.5 x 6-22.5 μm. *Spore germination* (Figs. 85 F-I, K, L) results in cylindrical, typically four-celled basidium, each basidial cell with one or more lateral sterigmata, 4-5 x 35-55 μm. *Basidiospores* (Fig. 85 J) apiculate, narrow allantoid or similar to the ballistospores in form, 1.5-2 x 6-7 μm, germinating by germ tube or by repetition.

Isolated from decayed wood, Canada. Known from the type culture only.

Ref.: Bandoni & Johri 1972.

Fig. 85 A-M. Culture and life cycle of *Tilletiaria anomala*, type (after Bandoni & Johri 1972; Reproduced from the Canad. J. Bot. 50, 1972, with the permission of the © holder and of Dr. R.J. Bandoni).

- **A.** Ballistospores, two of which are germinating by repetition.
- B. Fertile hyphal branch with fusion bridge.
- C. Start of teliospore formation.
- **D**, E. Mature teliospores with aculeate walls and septate terminal appendages. Note the intercalarly teliospore in Fig. D.
- F-I. Germinating teliospores with metabasidia.
- J. Basidiospores.
- K, L. Teliospores germinating by direct formation of hyphae.
- M. Life cycle of *Tilletiaria anomala*.



86. TOLYPOSPORELLA G.F. Atkinson,

Bull. Cornell Univ. 3(1):16, 1897.

Sori on leaves or leaf sheaths of plants in Poaceae. Spores with thickened outer walls, firmly agglutinated into spore balls. Spore germination results in a basidium with one-celled, pleurogenous ballisto-basidiospores. Host-parasite interaction apparatus lacking, hyphae mostly intercellular. Mature septa poreless.

Tolyposporella belongs to the Tilletiariaceae in the Georgefischeriales. It is close to *Phragmotaenium* from which it differs mainly in the presence of spore balls. Thirumalachar, Whitehead & O'Brien (1967) studied this genus and stated: "The chief characteristics of the genus were misinterpreted, and several leaf smuts with dark agglutinated spore masses were described as *Tolyposporella* species". They studied *T. brunkii* (Ell. & Gall.) G.P. Clinton, *T. chrysopogonis* G.F. Atk., *T. crepidis-rubrae* (Jaap) Cif., *T. irregularis* (Pazschke) Zundel, *T. linearis* (Berk. & Broome) L. Ling, *T. nolinae* G.P. Clinton, *T. obesa* (H. & P. Sydow) G.P. Clinton & Zundel, *T. obionum* (Speg.) Cif., *T. pachycarpa* (H. Sydow) L. Ling, *T. semenoviana* Lavrov, and *T. sporoboli* H.S. Jackson, and concluded that only the type species belongs to this genus. Indeed, most of these "*Tolyposporella*" species do not belong to this genus and the group needs a critical study by modern methods. Walker & Shivas (1998) placed *T. brunkii* into the genus *Jamesdicksonia* as *J. brunkii*. Vánky (2011('2012'):992) recognised 6 *Tolyposporella* species. Recently, for *T. pachycarpa* a new genus, *Tubisorus* Vánky & M. Lutz was described. *Type of the genus*:

Tolyposporella chrysopogonis G.F. Atkinson,

Bull. Cornell Univ. 3(1):16, 1897.

Type on *Chrysopogon nutans* (= *Sorghastrum nutans*), USA, Alabama, Auburn, autumn, collected several times by Duggar, i. a. autumn 1891, and by G.F. Atkinson, III.1892 (no special collection design.).

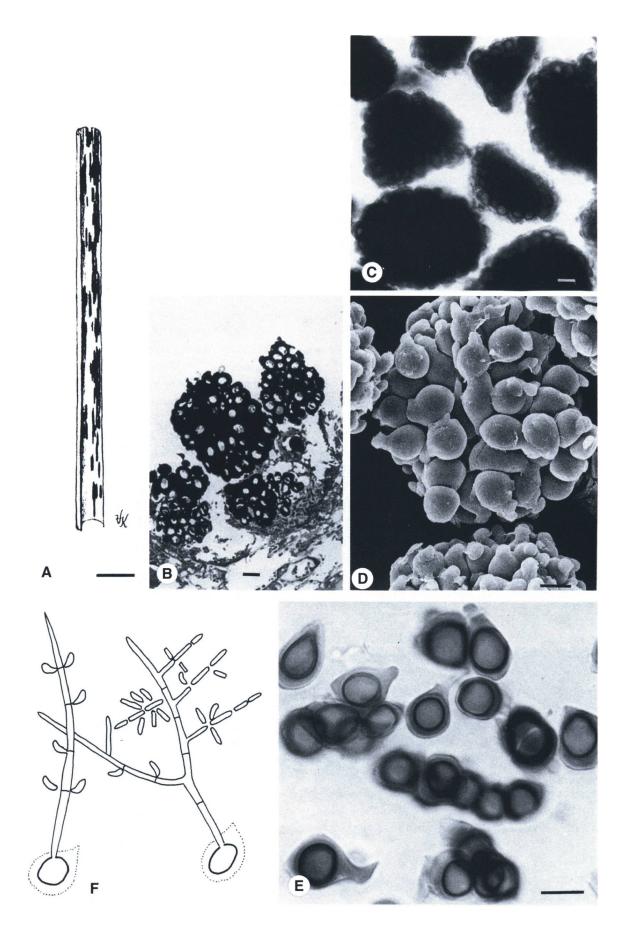
Sori (Figs. 86 A, B) on inner surface of leaf sheaths, by which they are concealed, forming linear, more or less confluent, at first subepidermal, later bursting striae filled with black, granular-agglutinated masses of spore balls. Spore balls (Figs. 86 B, C, D) subglobose, oblong, subpolyhedral, usually irregular, 40-80 x 50-175 μm, reddish to blackish brown, opaque, composed of numerous, firmly agglutinated spores, separating with difficulty. Spores (Figs. 86 D, E) subglobose, ovoid, usually irregular, (7-)8-9.5 x 8-13(-15) μm including the thin (c. 1 μm), dark endospore but excluding the irregular, 2.5-8(-14) μm thick, laminated, pale yellowish brown, smooth exospore which, on the outer spores of the ball may be excessively thickened forming long (up to 14 μm), often bent appendages; with such thickenings of the spore wall the spores may reach 30 μm in length. Spore germination (Fig. 86 F) results in branched, septate basidium producing laterally subclavate ballisto-basidiospores, 2-2.5 x 9-12 μm (Atkinson 1897:16, Thirumalachar, Whitehead & O'Brien 1967:392).

On Poaceae: Sorghastrum nutans (L.) Nash (Chrysopogon nutans (L.) Benth; Ch. avenaceus (Michaux) Benth; S. avenaceum (Michaux) Nash), and S. stipoides (Kunth) Nash; C Africa (Uganda), N America (USA).

Ref.: Atkinson 1897, Thirumalachar, Whitehead & O'Brien 1967.

Fig. 86 A-E. *Tolyposporella chrysopogonis* on *Sorghastrum nutans*, USA, Kansas, Riley Co, Kansas State College, Ashland Agronomy Farm, 1.X.1951, leg. C.T. Rogerson, HUV 2438 ex NY.

- A. Sori on the inner surface of a leaf sheath. Habit (Bar = 1 cm).
- **B.** T.S. of a sorus with developing spore balls (Bars = $10 \mu m$).
- C, D, E. Spore balls and spores in LM and in SEM (Bars = $10 \mu m$).
- **F.** Spore germination resulting in phragmobasidia with ballisto-basidiospores (after Thirumalachar, Whitehead & O'Brien 1967:392).



87. TOLYPOSPORIUM M. Woronin ex J. Schröter.

in Cohn, Cryptogamen-Flora von Schlesien 3(1):276, 1887.

TOLYPOSPORIUM Woronin, Abh. Senckenb. Naturf. Ges. 12:577, 1882('1881'), nom. nud. — Type: T. junci (J. Schröter) Woronin.

Sori naked on the surface of plants in Cyperaceae and Juncaceae, in floral organs, flowers or vegetative parts of the host plants, or subepidermal on the stems, formed by a black, at first agglutinated, later granular-powdery mass of spore balls. Spore balls composed of few to many, firmly or loosely united, dark-colored spores. Sterile cells absent. Spore germination results in phragmobasidia. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Woronin erected this genus for *Sorosporium junci* J. Schröter because its germination characteristics differ from those of Sorosporium saponariae, the type of Sorosporium. Over the years numerous fungi with spore balls have been included in the genus Tolyposporium (comp. Zambettakis & Joly 1973), which became heterogeneous containing species with widely variable morphology and biology. Of the 40 or so species that have been referred to as Tolyposporium, some belong to Thecaphora (incl. Glomosporium and Sorosporium), others to Cintractia, Entyloma, Eriomoeszia, Fulvisporium, Moesziomyces, Schizonella and Ustilago. Some proved to be mitosporic fungi, others to be Ascomycota (e.g. Tolyposporium montiae). Recently, the genus Tolyposporium was split into 2000b): three genera (Vánky, 1. Restiosporium Vánky Restionaceae. 2. Moreaua Liou & H.C. Cheng, emend. Vánky, on Cyperaceae, and 3. Tolyposporium on Juncaceae and Cyperaceae, with three species in the Anthracoideaceae. These are: 1. T. isolepidis (Vánky) Vánky & M. Lutz, and 2. T. neillii (G. Cunn.) Vánky & McKenzie, both on Ficinia (Isolepis), and 3. The Type of the genus:

Tolyposporium junci (J. Schröter) M. Woronin ex J. Schröter, in Cohn, *Cryptogamen-Flora von Schlesien 3(1)*:276, 1887.

Sorosporium junci J. Schröter, Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss. 1869/72:6, 1869. — Tolyposporium junci (J. Schröter) Woronin, Abh. Senckenb. Naturf. Ges. 12:577, 1882('1881') (invalid name, the genus Tolyposporium having been validly published first in 1887). — Type on Juncus bufonius, Germany, Silesia, Carlowitz near Breslau [= Poland, Karlowice near Wrocław], IX.1867, leg. J. Schröter; isotypes in Schneider, Herb. schles. Pilze no. 94, HUV 7207!

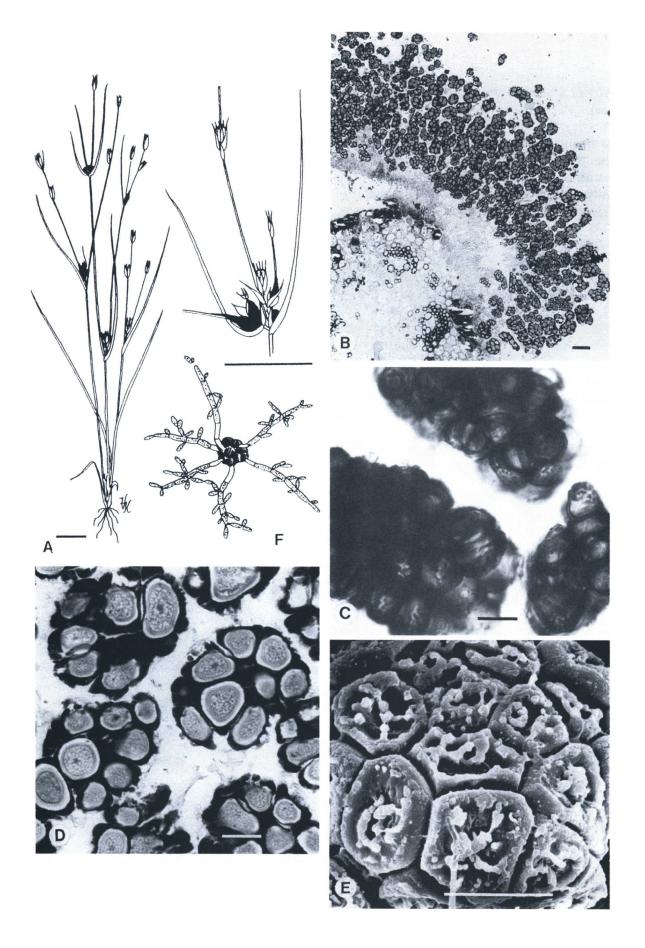
Sori (Fig. 87 A, B) naked, tumor-like, as a black, agglutinated to granular spore mass, composed of spore balls localized in the flowers (often involving only part of the flowers, the capsule, or only the base of the flower and spreading to the adjacent bracts and rachis), less often at the base of the stems and basal leaves. *Spore balls* (Figs. 87 C, D, E) persistent, varying in shape and size, globose, subglobose, elongate or irregular, 16-50(-80) μm long, opaque, dark reddish brown to blackish brown, composed of 3-40 (or more?) spores (For spore ball formation see Vánky 1994:273). *Spores* (Figs. 87 C, D, E) subglobose to more or less angular, often subcuneiform and irregular, 6-13 x 8-17(-20) μm, dark yellowish brown to blackish brown, smooth on the contact surface and with irregular warts on the free, slightly convex surface. The wall is unequally thickened (0.5-4 μm) and two-layered; in TEM the inner layer shows a gray, uniformly thick (0.6-0.8 μm) central part and a light, uneven (0.2-1.2 μm), peripheral part, sharply delimited from the outer layer which appears black, uneven (0.2-2.5 μm), without apparent structure. *Spore germination* (Fig. 87 F), after a resting period, in water, results in four-celled basidia with basidiospores born at the septa (Woronin 1882('1881'):575, Brefeld 1895:150, Pl. IX, figs. 13-24).

On Juncaceae: Juncus bufonius L., J. capitatus Weigel; Europe, N America (USA).

Ref.: Zambettakis & Joly 1973, Thirumalachar & Neergaard 1978('1977'), Vánky 1977, 2000b.

Fig. 87 A-E. Tolyposporium junci on Juncus bufonius, Vánky, Ust. exs. no. 107, HUV 2475.

A. External sori. Habit and enlarged some sori (Bars = 1 cm). **B.** T.S. of a sorus with spore balls in different developmental stages (Bar = 10 μ m). **C, D, E.** Spore balls and spores in LM, in TEM and in SEM (Bars = 10 μ m). **F.** Spore germination (Brefeld 1895).



88. *TRACYA* H. & P. Sydow, *Beibl. Hedwigia*, *40*:(3), 1901.

CORNUELLA Setchell, Proc. Amer. Acad. Arts 26:19, May 1891 (non Cornuella Pierre, January 1891, q.e. Sapotaceae).

Sori as finely punctate, rather indefinite spots in vegetative parts of aquatic plants in Hydrocharitaceae and Lemnaceae. Spore balls embedded in the host tissue, persistent, composed of a central network of branched, septate, hardened hyphae and a peripheral layer of firmly adhering spores. No sterile cortex. Spore germination of Tilletia-type. Host-parasite interaction by complex interaction apparatus with cytoplasmic portions, haustoria absent. Septal pore is simple, with two membrane caps.

Tracya, in the Doassansiaceae, forms a morphologically, ecologically and phylogenetically natural group together with *Burrillia*, *Doassansia*, *Entylomaster*, *Heterodoassansia*, *Nannfeldtiomyces*, *Narasimhania*, *Pseudodermatosorus*, *Pseudodoassansia* and *Pseudotracya*. Two species of *Tracya* are known: 1. *T. hydrocharidis* Lagerh. on *Hydrocharis* species (Hydrocharitaceae) from Europe and Asia, and 2. The *type of the genus*:

Tracya lemnae (W.A. Setchell) H. & P. Sydow, *Beibl. Hedwigia 40*:(3), 1901.

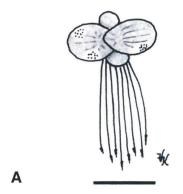
Cornuella lemnae Setchell, Proc. Amer. Acad. Arts 26:19, 1891. — Lectotype on Lemna polyrhiza (= Spirodela polyrhiza), USA, (design. by Zundel 1953:304) Massachusetts, Middlesex Co., Cambridge, Glacialis Pond, 30.VI.1889, leg. W.A. Setchell, PC.

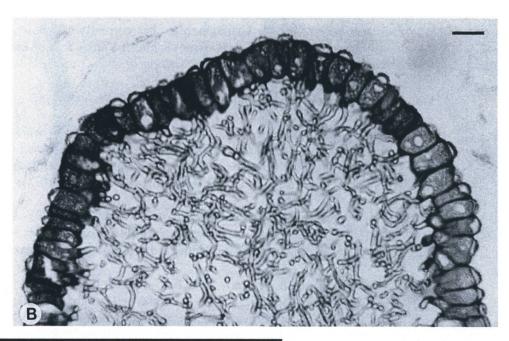
Sori (Fig. 88 A) in fronds, initially as pale yellowish green, later pale yellowish brown, indefinite areas, with spore balls embedded in the host tissue appearing as gregarious or scattered, pale brown, minute pustules. Spore balls (Figs. 88 B, C) globose to elongate or slightly irregular, 65-240(-320) μm long, composed of numerous spores arranged in a single, peripheral layer, and a central network of branched, hardened hyphae. Spores (Figs. 88 B, C) firmly united, radially elongate, polyhedral, 5-10.5 x 9.5-14 μm, pale yellowish brown; wall 0.8-1.2 μm thick, finely verruculose on the outer, free surface, smooth on the contact surfaces, inner, free wall continues into the pale yellowish brown, 1.5-2.3 μm wide hyphae, which form the central, interwoven mycelial network. Spore germination of Tilletia-type (Setchell 1892).

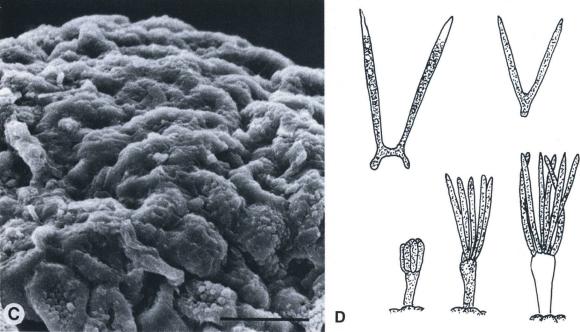
On Lemnaceae: Spirodela polyrhiza (L.) Schleid. (Lemna polyrhiza L.); Europe, N America.

Ref.: Setchell 1892, Reukauf 1906, Liro 1938, Vánky 1981b.

- **Fig. 88 A-C.** *Tracya lemnae* on *Spirodela polyrhiza*, Hungary, Bács-Kiskun Co, "Tőserdő" near Kapásfalú, 8.XI.1978, leg. J. Gönczöl, HUV 7798.
- A. Sori in the fronds as indistinct spots with minute dots, the spore balls embedded in the host tissue. Habit (Bar = 1 cm).
- **B.** T.S. of a spore ball in LM (stained), showing the central network of hardened hyphae and the peripheral layer of spores (Bar = $10 \mu m$).
- C. The surface of a spore ball in SEM (Bar = $10 \mu m$).
- **D.** Spore germination of *Tracya hydrocharidis* Lagerh. (after Setchell 1892, Pl. I).







89. TRANZSCHELIELLA N.N. Lavrov,

Trudy Biol. Naučno-Issl. Inst. Tomsk. Gosud. Univ. 2:29, 1936.

Sori on stems or aborted inflorescence branches of plants in Poaceae, superficial, covered by brown, powdery spore mass, naked or with an ephemeral peridium. Infection systemic. *Spores* solitary, pigmented (brown), operculate or not, usually small-sized. *Spore germination* results in phragmobasidia. *Host-parasite interaction* by intracellular hyphae lacking interaction apparatus. Mature *septa* poreless.

Lavrov described *Tranzscheliella* on the basis of the two, small, supposed "cells" attached at opposite sides of the spores. What Lavrov considered to be cells are actually the oppositely situated opercula (circularly broken parts of the thick exospore, standing off from the spore). This character alone is maybe insufficient for recognizing a separate genus. However, *Tranzscheliella*, together with the closely related "*Ustilago*" *hypodytes* complex, differs markedly, in several aspects from *Ustilago hordei*, the type of the genus *Ustilago*. It was studied by Vánky (2003b:2-4). *Tranzscheliella*, in the Ustilaginaceae, has currently 17 known species (comp. Vánky 2011('2012'):1002) including the cosmopolitan *T. hypodytes* (Schltdl.) Vánky & McKenzie complex, on numerous grass genera. *Type of the genus: T. otophora* Lavrov = *T. williamsii*.

Tranzscheliella williamsii (D. Griffiths) J.M. Dingley & W. Versluys, *New Zealand J. Bot. 15*:477, 1977.

Sorosporium williamsii Griffiths, Bull. Torrey Bot. Club 29:296, 1902. — Ustilago williamsii (Griffiths) Lavrov, Trudy Biol. Naučno- Issl. Inst. Tomsk Gosud. Univ. 2:22, 1936. — Ustilago williamsii (Griffiths) G.W. Fischer & Hirschhorn, Mycologia 37:253, 1945 (comb. superfl.). — Type on Stipa richardsonii, USA, Wyoming, Big Horn Mts., VIII.1898, leg. T.A. Williams & D. Griffiths; isotypes in Griff., W. Amer. fgi. no. 306, HUV 1081!

Ustilago appendiculata Spegazzini, Anales Mus. Nac. Buenos Aires, Ser. 3, 12:288, 1909. — Tranzscheliella appendiculata (Speg.) Lavrov, Trudy Biol. Naučno- Issl. Inst. Tomsk. Gosud. Univ. 2:30, 1936. — Type on Stipa chrysophylla (= S. humilis), Argentina, Cacheuta Mt., near Mendoza, II.1908, leg. C. Spegazzini, LPS 3004. (Syn. by Fischer & Hirschhorn 1945:253).

Tranzscheliella otophora Lavrov, Trudy Biol. Naučno- Issl. Inst. Tomsk. Gosud. Univ. 2:30, 1936. — Ustilago otophora (Lavrov) Gutner, Golovnevye griby:52, 1941. — Lectotype (design. by Vánky 1985a:256) on Stipa pennata, Turkmeniya, Firjoza, VI.1924, leg. Chernvakovskaya. (Syn. by Vánky 1985a:256).

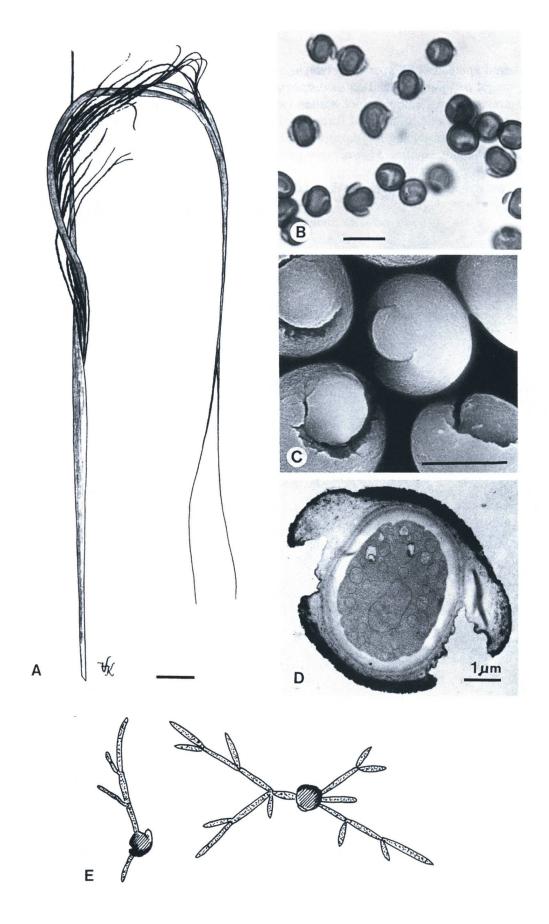
Sori (Fig. 89 A) as in *Tranzscheliella hypodytes*, surrounding upper internodes and aborted inflorescence axes, initially protected by leaf sheaths, later naked, blackish brown, powdery, lacking a peridium. Infection systemic, attacked plants usually not flowering. *Spores* (Figs. 89 B, C, D) globose to subglobose, 6-8 x 7-10 μm, olive-brown, exospore often deeply cracked, bearing two hyaline, winged or cup-like, 1-2.5 μm thick, bipolar appendages; in SEM typically operculate. *Spore germination* (Fig. 89 E) results in 4-celled, often branched basidium producing elongate basidiospores laterally and apically.

On Poaceae: Achnatherum, Austrostipa, Oryzopsis and on at least 34 Stipa species; Europe, N Africa, Asia, New Zealand, N & S America.

Ref.: Lavrov 1936, Dingley & Versluys 1977, Vánky & McKenzie 2002b, Vánky 2003b.

Fig. 89 A-D. Tranzscheliella williamsii on Stipa borysthenica, Vánky, Ust. exs. no. 324 (as Ustilago williamsii), HUV 9562.

- A. Sori on the surface of aborted panicle branches. Habit (Bar = 1 cm).
- B, C, D. Spores in LM, in SEM (Bars = 10 µm), and in TEM (TEM picture by R. Bauer).
- E. Spore germination (after Fischer & Hirschhorn 1945:254, Kolk 1943:322).



90. TRICHOCINTRACTIA M. Piepenbring,

Canad. J. Bot. 73:1095, 1995.

Sori in scattered spikelets of Cyperaceae (*Rhynchospora*), forming swollen, sac-like bodies, covered by a thick, whitish, fungal peridium, opened on its distal part, filled with a dark brown, dusty mass of spores. From the soral base, groups of long, smooth, thick-walled sterile cells radiate into the spore mass. *Spores* when young in globose groups, later single, pigmented (brown, without red or violet tint), ornamented. *Spore germination* results in phragmobasidia producing basidiospores or hyphae. *Host-parasite interaction* by intracellular hyphae, coated by an electron-opaque matrix. Mature *septa* poreless. *Type of the genus: T. utriculicola*.

Trichocintractia is a unispecific genus in the Anthracoideaceae, order Ustilaginales.

Trichocintractia utriculicola (P. Hennings) M. Piepenbring,

Canad. J. Bot. 73:1095, 1995.

Cintractia leucoderma (Berk.) Henn. forma utriculicola Hennings, Hedwigia 34:336, 1895. — Cintractia utriculicola (Henn.) G.P. Clinton, J. Mycol. 8:143, 1902. — Type on Rhynchospora gigantea, Brazil, Prov. Sta. Catharina Prov., Blumenau, leg. A. Möller.

Ustilago conglobata Cooke (? nom. herb.) on Rhynchospora aurea (= R. corymbosa), without locality, 11.XII.1885, leg. Clarke, K!

Cintractia axicola (Berk.) Cornu forma spicularum Juel, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 23(10):7, 1897. — Cintractia spicularum (Juel) Raciborski, Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math. Nat. 1909:353, 1909. — Type on Rhynchospora sp., Brazil, Rio Grande do Sul, Pôrto Alegre, 7.XI.1892, leg. C.A.M. Lindman. (Syn. by Zundel 1953:38).

Sori (Fig. 90 A) in some spikelets of an inflorescence, replacing the flowers, ovoid, 2-2.5 x 3-5 mm, covered by a grayish white, thick peridium of fungal origin, initially closed, later rupturing apically disclosing the black, powdery mass of spores. *Spores* (Figs. 90 C, D) when young in globose groups between the sterile fungal cells, later single, slightly flattened, in side view broadly elliptic to slightly irregular, 10-13 μm wide, in plane view circular to broadly elliptic, 11-15 × (11-)12-16(-17.5) μm, medium olive-brown; wall 1-2(-2.5) μm thick, with a c. 0.5 μm thin, rounded area of 4-6.5 μm diameter on the flattened sides, where the spore color is also paler, surface in LM apparently smooth to minutely, densely punctate, in SEM finely, densely verruculose. *Sterile fungal cells* (Fig. 90 D) originating from the host tissue at the base of the sorus, radiating into the spore mass, numerous, in groups but not sticking together, long cylindrical, without septa, 5 μm wide and up to 600 μm long; wall up to 2 μm thick, less at the cell tip, smooth. *Spore germination* (Fig. 90 E) results in phragmobasidia producing basidiospores or hyphae.

On Cyperaceae: *Rhynchospora asperula* (Nees) Steud., *R. corymbosa* (L.) Britton (*R. aurea* Vahl), *R. gigantea* Link, *R. holoschoenoides* (L.C. Rich.) Herter (*R. cyperoides* (Seward) Mart.), *R. triflora* Vahl; cosmopolitan in the tropics.

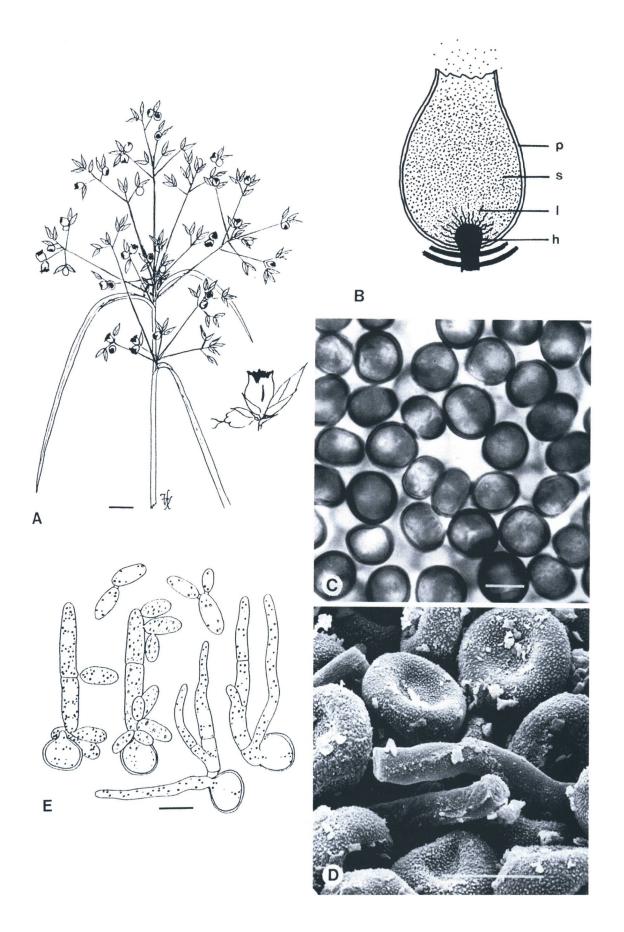
For detailed description and illustration of sorus structure and spore formation see also Juel (1897:7-9, Pl. I, fig. 2, Pl. II, figs. 6-7; as *Cintractia axicola* forma *spicularum*).

Ref.: Juel 1897, Ling 1950b, Piepenbring 1995.

Fig. 90 A-E. *Trichocintractia utriculicola* on *Rhynchospora corymbosa*. A, C, D. Vánky, Ust. exs. no. 813 (as *Cintractia utriculicola*), HUV 15705.

A. Sori in some spikelets of the inflorescence. Habit (Bar = 1 cm). Enlarged a triplet of spikelets: a healthy spikelet (to the right), a young, lobed, unopened sorus (to the left), and a mature, opened sorus with the cupshaped peridium (in the middle).

- **B.** Schematic L.S. of a sorus, p = peridium, s = spores, l = long, sterile cells, h = host tissue.
- C, D. Spores in LM and in SEM. In SEM picture also two, cylindrical, sterile cells.
- E. Spore germination (B, E. after Piepenbring 1995).



91. TRIODIOMYCES A.R. McTaggart & R.G. Shivas,

in McTaggart, Shivas, Geering, Vánky & Scharaschkin, Persoonia 29:131, 2012c.

Sori in culms or inflorescences of *Triodia* (Poaceae). Columella, spore balls and sterile cells absent. Spore germination of Ustilago-type.

Triodiomyces, in the Ustilaginaceae, has five known species, all on Triodia in Australia: 1. T. inaltilis (Vánky & A.A. Mitch.) McTaggart & R.G. Shivas, 2. T. lituanus (R.G. Shivas, Vánky & Cunningt.) McTaggart & R.G. Shivas, 3. T. lunatus (R.G. Shivas, McTaggart & Vánky) McTaggart & R.G. Shivas, 4. T. triodiae (Vánky) McTaggart & R.G. Shivas, and 5. The type of the genus:

Triodiomyces altilis (H. Sydow) A.R. McTaggart & R.G. Shivas, in McTaggart, Shivas, Geering, Vánky & Scharaschkin, *Persoonia 29*:131, 2012c.

Ustilago altilis H. Sydow, Ann. Mycol. 35:23. 1937. — Lectotype on Triodia sp., Australia, Northern Territory, between Liddels Hill and Ayers Rock (Uluru). VI.1935, comm. J.B. Clealand, (design. by Vánky & Shivas 2008:233) BRIP 7884. (The holotype was lost in B. A neotype was designated by Vánky (1997:166). However, two isotypes were found by Shivas, one of which was proposed as lectotype); isolectotypes ADW 1556, 1593, NTPPMH 3520.

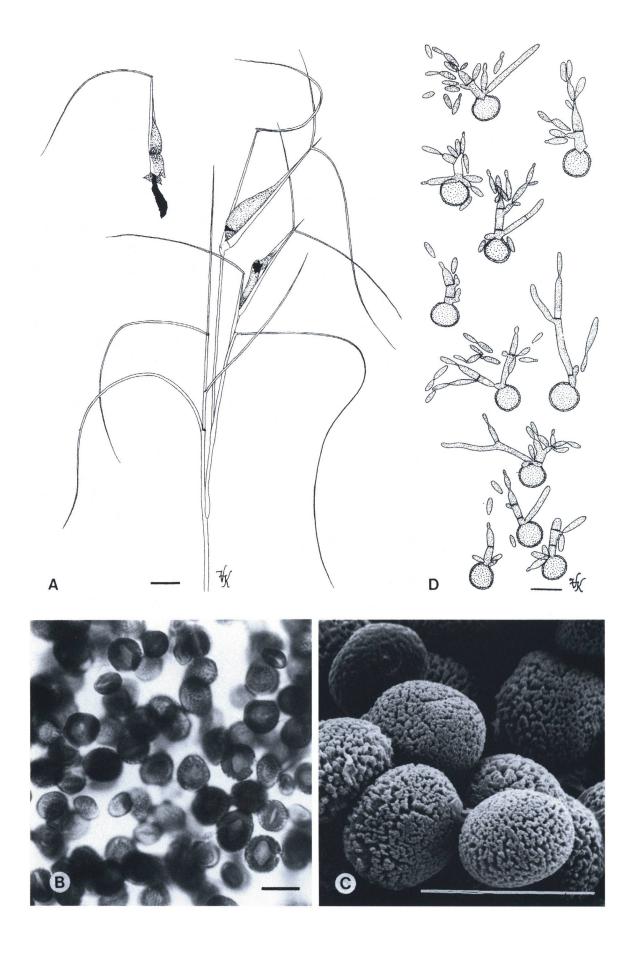
Sori (Fig. 91 A) in distal part of the stems (destroying the inflorescence?), initially concealed by leaf sheaths and covered by a grey peridium of host origin lined by mycelia. Sori fusiform, bullate, $0.3-1 \times 1-5$ cm. Infected plants somewhat stunted and congested. The peridium ruptures irregularly exposing the black, semi-agglutinated mass of spores surrounding the stem of the host. *Spores* (Figs. 91 B, C) globose, subglobose to broadly ellipsoidal, $7-11 \times 7-12$ µm, reddish brown; wall 2.5-3 µm thick, densely, prominently verrucose. Spore formation was observed on the inner surface of the peridium. Young spores in chains, formed within the ramified sporogenous hyphae (Vánky 1997:167).

On Poaceae: Triodia basedowii Pritz., T. bitextura Lazarides (Plectrachne pungens (R.Br.) C.E. Hubb.), T. brizoides N.T. Burb., T. burbidgeana S.W.L. Jacobs, T. epactia S.W.L. Jacobs, T. irritans R.Br., T. melvillei (C.E. Hubb.) Lazarides (Plectrachne melvillei C.E. Hubb.), T. microstachya R.Br., T. mitchellii Benth. (T. hostilis Domin), T. pungens R.Br., T. salina Lazarides, T. schinzii (Henrard) Lazarides (Plectrachne schinzii Henrard), T. stenostachya Domin, Triodia sp.; Australia.

Ref.: McTaggart, Shivas, Geering, Vánky & Scharaschkin 2012c.

Fig. 91 A-C. Triodiomyces altilis on Triodia pungens R.Br., Vánky, Ust. exs. no. 418

- A. Sori in distal part of the stems. Habit (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$).
- **D.** *Triodiomyces triodiae* on *Triodia pungens* R.Br. Germinating spores (on MYP, at room temp., after one day; Bar = $10 \mu m$).



92. *TUBISORUS* K. Vánky & M. Lutz, *Mycol. Balcan.* 8:131, 2011.

Sori tubular on host plants in the Poaceae, filled with dark, granular powdery mass of spore balls, columella and sterile cells lacking. Spore balls composed of spores only. *Spores* pigmented (brown, without violet or red tint). The proper spore is hyaline and embedded in a thick, hyaline, gelatinous substance, coated by a thin, pigmented, ornamented outer layer of spore wall. *Type of the genus:*

Tubisorus pachycarpus (H. Sydow) K. Vánky & M. Lutz *Mycol. Balcan.* 8:131, 2011.

Sorosporium pachycarpum Syd., in H. Sydow & Petrak, Ann. Mycol. 26:431, 1928. — Tolyposporella pachycarpa (Syd.) L. Ling, Sydowia 3:133, 1949. — Endosporisorium pachycarpum (Syd.) Vánky, Mycotaxon 56:213, 1995. — Syntype on Rottboellia ophiuroides (= Mnesithea rottboellioides), Philippines, Luzon, Pampanga Prov., Stotsenberg, XI.1923, coll. M.S. Clemens 2313, BPI 180089! (Another syntype is probably lost).

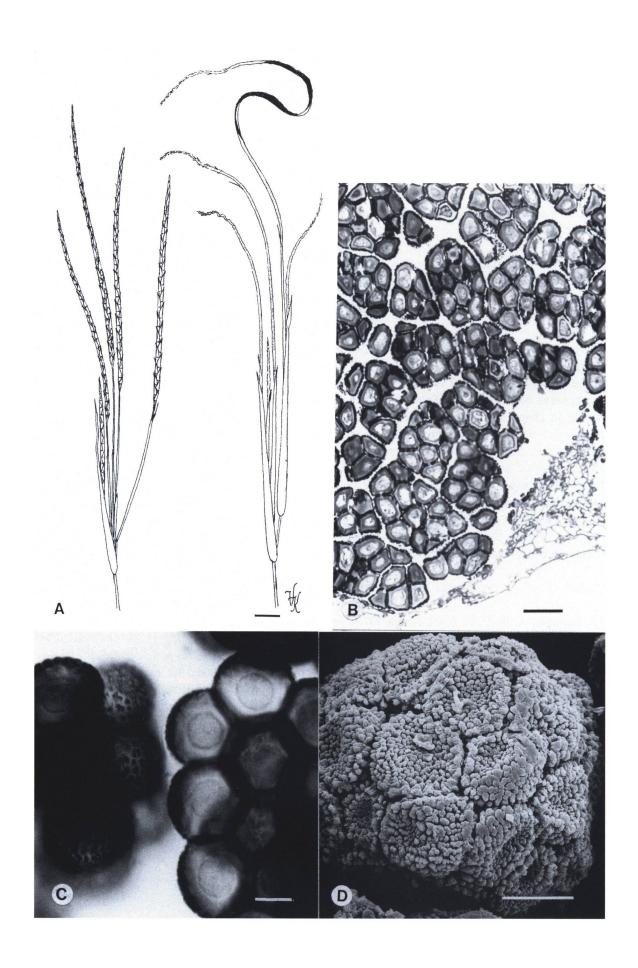
Sori (Figs 92 A, B) in much elongated axis of the spikes with aborted spikelets, tubular, 0.5-1.5 mm wide, up to 20-25 cm long, yellowish to grayish brown, at maturity rupture longitudinally, on several places between the veins, exposing the black, granular-powdery mass of spore balls. Spore balls (Figs 92 C, D, E) globoid, long ellipsoidal to irregular, composed of 5–50 or more spores, apparently loose but rather permanently connected, $25-50(-65) \times 45-100(-150)$ µm, dark olivaceous brown. Spores (Figs. 92 C, D, E) subglobose, ovoid or irregular with one or several flattened contact sides, $12-20 \times 16-24$ µm, olivaceous brown; wall 3-layered: outer layer 1.5-2 µm thick, pigmented, densely provided with irregular, prismatic warts, c. 1 µm high on the free surface, smaller and finer on the contact sides; middle layer hyaline, gelatinous, homogenous, 2.5-7 µm thick; inner layer 0.5-1.5 µm thick, smooth, surrounding the finely granular, hyaline proper spores which in squashed spores are eliberated. These are subglobose, broadly ellipsoidal, ovoid, subpolyhedrally irregular or elongated, $(7-)8-10.5 \times 9-14.5$ µm; wall 0.5-1 µm thick, composed of a very thin inner layer and and a hyaline sheath, smooth. Spore germination unknown.

On Poaceae: *Mnesithea rottboellioides* (R.Br.) de Koning & Sosef (*Coelorachis rottboellioides* (R.Br.) A. Camus; *Manisuris rottboellioides* (R.Br.) Kuntze; *Rottboellia ophiuroides* Benth.); Australia, Papua New Guinea, Philippines.

Ref.: Sydow & Petrak 1928, Vánky & Lutz 2011.

Figs 92 A-D. Tubisorus pachycarpus on Mnesithea rottboellioides (Papua New Guinea, HUV 16772).

- **A.** Sori in elongate, tubular axis of the spikes with aborted spikelets. Habit. Healthy spikes with spikelets (left) (Bar = 1 cm).
- **B.** Semi-thin, stained, transversal section of a part of a sorus with sectioned spore balls and spores (Bar = $25 \mu m$).
- C, D. Spore balls and spores in LM and in SEM. On the LM picture, note the three layers of the spores, respectively the proper spores embedded in a thick, gelatinous layer coated by the pigmented, ornamented, thin outer layer of the wall (Bars = $10 \mu m$).



93. *ULEIELLA* J. Schröter, *Beibl. Hedwigia 33*:(65), 1894.

ULEA J. Schröter, Bot. Centralbl. 50:42, 1892, nom. nud.

Sori formed in Gymnospermae (Araucariaceae), in the top of the shoots, in some young inflorescences of a tree as naked, dark brown, powdery masses of spore-complexes. Spore-complexes varying in shape and size, composed of a thick, pigmented (yellowish brown), reticulate coat surrounding one to usually several spores embedded in a hyaline mass. Spore germination results in a short, later ramifying basidium producing apically ovoid, hyaline basidiospores. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Uleiella, in the Uleiellaceae of the Ustilaginales, has two known species, both on *Araucaria* species in S America: 1. *U. chilensis* Dietel & Neger, and 2. The *type of the genus*:

Uleiella paradoxa J. Schröter,

Beibl. Hedwigia 33:(65), 1894.

Ulea paradoxa J. Schröter, *Bot. Centralbl. 50*:42, 1892 (nom. subnud.). — Type on *Araucaria imbricata*, Brazil, Sierra Geral., V.1891, leg. E. Ule; isotypes in Rbh., Fgi. eur. no. 3940, HUV 12257!

Sori in the top of the shoots, in young female and male inflorescences as naked, dark brown, powdery masses of spore-complexes on the surface of the basal part of the scales and in the ovules. Spore-complexes (Figs. 93 B, C, D) varying in shape and size, globose, ellipsoidal to slightly irregular, rarely elongate, 20-35 x 22-44 μm, composed of a 2.5-5.5 μm thick, densely, finely reticulate, yellowish brown cover surrounding 1-16 (or more?) spores embedded in a hyaline mass. Spores (Figs. 93 B, C) varying in shape and size, globoid, ellipsoidal, rhomboidal to slightly irregular, rarely elongate, 5-11 x 6-13.5(-20) μm, if single then larger (12-16 x 13-20 μm), with a smooth, evenly c. 0.5 μm thick, pale yellowish brown wall surrounded by a 0.5-1 μm thick, hyaline sheath. By hard pressure, the cover ruptures and the spores are liberated (Fig. 93 B; see also Thirumalachar 1949:342, fig. 4). Spore germination (of U. chilensis) results in a short, later branching basidium producing apically ovoid, hyaline, yeast-like basidiospores (Butin & Peredo 1986:68).

On Araucariaceae: Araucaria angustifolia (Bertol.) Kuntze, A. imbricata Pav.; S America (Brazil, Chile).

Ref.: Schröter 1892, 1894, Dietel 1897b, Thirumalachar 1949, Mattos 1972, Butin & Peredo 1986.

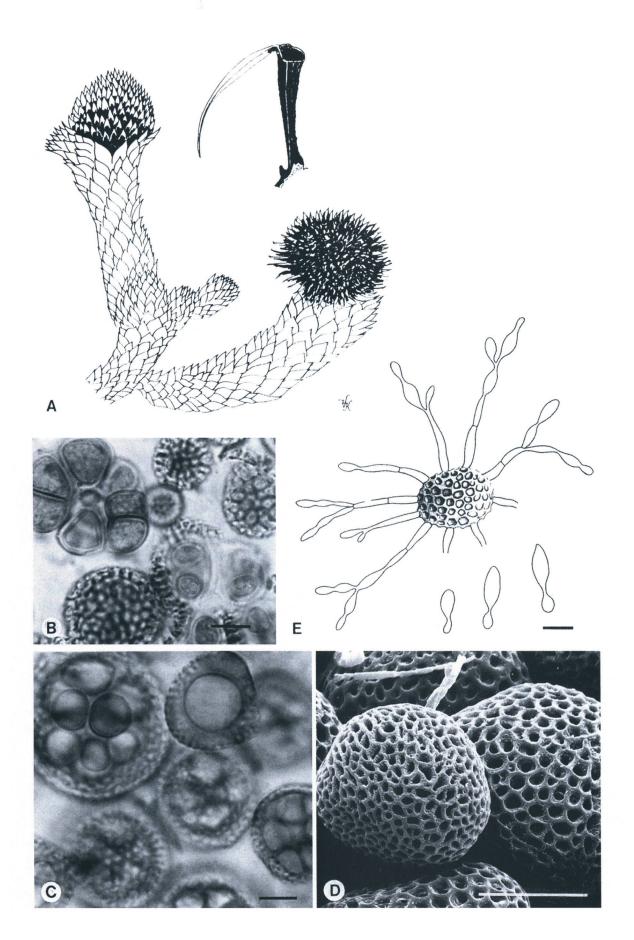
Fig. 93. Uleiella. A, B, C, E. U. chilensis, D. U. paradoxa.

A. Sori of *Uleiella chilensis* Dietel & Neger on the top of the shoots in young inflorescences of *Araucaria araucana* (Mol.) C. Koch, Chile, Lago Gualletue, 14.III.1985, leg. H. Butin, HUV 12249. Enlarged a scale with the naked, dark sorus on its proximal half. **B, C.** Spore-complexes with one- to many spores surrounded by a thick, reticulate cover in LM. In B some spore-complexes are squashed and the spores liberated.

- **D.** The finely, deeply reticulate cover of the spore-complexes of *Uleiella paradoxa* on *Araucaria imbricata* in SEM, lectotype, Rbh., Fgi. eur. no. 3940, HUV 12257.
- E. Spore-complex with enclosed germinating spores of *U. chilensis* (in water, at room temp., after 1 day. Bar = $10 \mu m$. Germination and drawing by H. Butin, Braunschweig, Germany).

For nomenclature and preference of *Uleiella J. Schröter* (1894) versus *Ulea J. Schröter* (1892), see Vánky 2001b.

It is not satisfactorily clarified what the rounded, reticulate, yellowish brown propagules of this fungus, with several, pale yellowish brown units inside represent. Until their origin and kind is known, I am calling them "spore-complexes" with one to usually several spores inside.



94. UROCYSTIS L. Rabenhorst ex L. Fuckel, nom. cons.

Jahrb. Nassauischen Vereins Naturk. 23-24:41, post 18.II.1870.

GRANULARIA Sowerby, Coloured figures of English fungi, etc., Suppl., Pl. 440, 1809, non Roth, 1791 (= Nidularia), nec Sacc. & Ellis ex Sacc., 1882 (= Mitosporic fungi). — Type: G. violae Sowerby (= Ur. violae). UROCYSTIS Rabenhorst, Herb. viv. myc. ed. 2, no. 393, 1857 (nom. nud.).

TUBURCINIA E. Fries, Syst. Myc., Vol. 3, sect. 2:439, 1832. — Type: T. orobanches (Mérat) Fr. (= Urocystis orobanches (Mérat) A.A. Fisch. Waldh.) on Orobanche ramosa L.

POLYCYSTIS Léveillé, Ann. Sci. Nat. Bot., Sér. 3, 5:269, 1846, non (Kützing) Kützing, 1849, q.e. Algae. — Type: P. pompholygodes Lév. on different hosts.

POLYSACCOPSIS Hennings, Beibl. Hedwigia 37:(206), 1898. — Type: P. hieronymi (J. Schröter) Henn. (= Urocystis hieronymi J. Schröter) on Solanum sp.

GINANNIELLA Ciferri, Fl. Ital. Crypt., Pars I. Fungi, Fasc. 17:150, 1938. — Type: G. trientalis (Berk. & Broome) Cif. (= Urocystis trientalis (Berk. & Broome) B. Lindeb.) on Trientalis europaea L.

Sori mostly in leaves and stems, sometimes in flowers or seeds, less often in roots of both mono- and dicotyledonous host plants, as brown or blackish brown streaks, spots, swellings or galls, containing a mass of spore balls, usually powdery. Infection usually systemic. Spore balls persistent, composed of one to several, pigmented (brown), fertile spores, surrounded by paler and smaller sterile cells. Spore germination of Tilletiatype. Anamorph (Paepalopsis Kühn) present in some species. Host-parasite interaction (Fig. 9, p. 24) by haustoria with enlarged interaction zones. Septal pore simple, with membrane caps and two non-membranous plates closing the pore.

Urocystis is a natural, well-delimited genus in the Urocystidaceae with c. 170 known species parasitizing 31 host plant families, both mono- (16) and dicotyledonous (15) ones. Species delimitation is often difficult because of overlap of the scanty morphological characters of the spore balls, spores and sterile cells. *Urocystis* was studied by Liro (1922, as *Tuburcinia*). *Type of the genus*:

Urocystis occulta (K.F.W. Wallroth) G.L. Rabenhorst ex L. Fuckel, Jahrb. Nassauischen Vereins Naturk., 23:41, 1870.

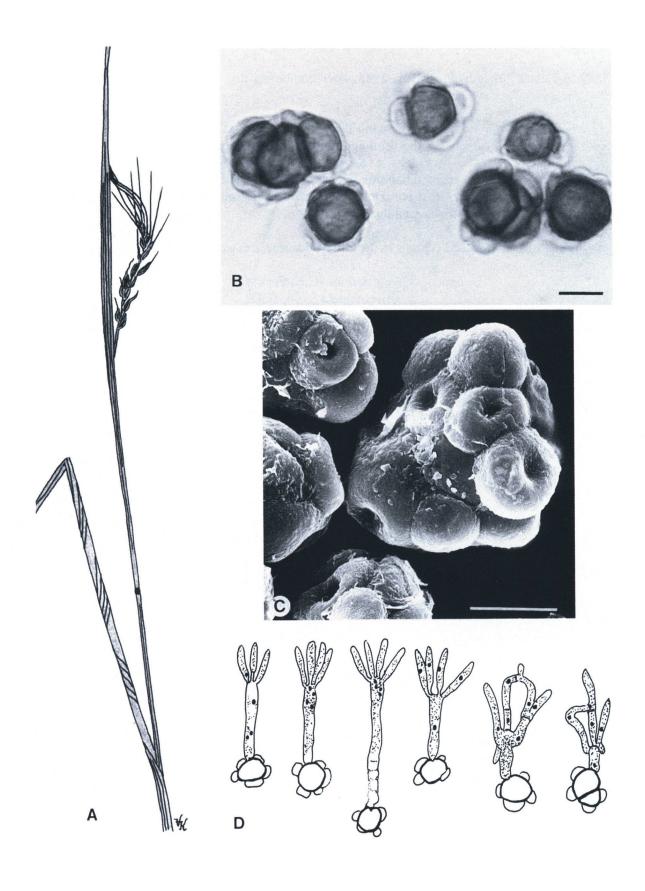
For nomenclatural and taxonomic synonyms, such as *Erysibe occulta* Wallr. α *secales* Wallr., *Polycystis occulta* (Wallr.) Schltdl., *Ustilago occulta* (Wallr.) Rabenh., *Urocystis occulta* (Wallr.) Rabenh., *Tuburcinia occulta* (Wallr.) Liro, as well as *Uredo parallela* Berk., *Tuburcinia hordei* Cif., and *T. secalis* Uljan., all on *Secale cereale*, see Vánky, *Smut Fungi of the World*, 2011('2012'):1085.

Sori (Fig. 94 A) in deformed leaves, sheaths, culms and spikes, appearing as long, sometimes confluent streaks, at first lead-colored, covered by the epidermis which ruptures longitudinally exposing the reddish black, dusty mass of spore balls. Spore balls (Figs. 94 B, C) subglobose, ovoid to irregular, (10.5-)13.5-20 x (12-)16-30(-40) μm, composed of 1-3(-5) spores surrounded by a usually incomplete layer of sterile cells. Spores (Figs. 94 B, C) varying in shape and size, subglobose, ovoid, elongate to irregular, often with flattened sides, (8-)10-13.5(-16) x (11-)13-20(-22.5) μm, reddish brown, contents finely granular; wall smooth. Sterile cells (Figs. 94 B, C) subglobose, ovoid to irregular, 6-13 μm long, light yellow, smooth. Spore germination (Fig. 94 D) results in aseptate basidia of variable length, bearing (2-)4-6, apical, elongate basidiospores. Meiosis and subsequent nuclear divisions take place in the basidium. Normally, each basidiospore receives one nucleus. After fusion of two compatible basidiospores, a dikaryotic infection-hypha results (Stakman, Cassel & Moore 1934).

On Poaceae: Secale cereale L. (cult.), ?S. montanum Guss.; cosmopolitan.

Ref.: Cooke 1877, Prillieux 1880a, 1880b, Liro 1922, 1938, Stakman, Cassel & Moore 1934, Zundel *et al.* 1940, Ulbrich 1940, Hirschhorn 1942, Massenot 1953, Nagler 1987, Nagler & Oberwinkler 1984, 1989.

Fig. 94 A-D. *Urocystis occulta* on *Secale cereale*, A-C. Hungary, Cegléd, 18.VI.1930, leg. B. Husz, HUV 2886. A. Sori in leaves, leaf sheaths and culms forming long striae. Habit. **B, C.** Spore balls, spores and sterile cells in LM and in SEM (Bars = $10 \mu m$). **D.** Spore germination (Stakman, Cassel & Moore, 1934:876).



95. USTACYSTIS G.L. Zundel,

Mycologia 37:796, 1945.

WHETZELIA Zundel, Mycologia 37:371, 1945, later homonym, non Whetzelia Chardón & Toro, 1934 (a genus of Dothideaceae, Ascomycota).

Sori in leaves of plants in Rosaceae, following the veins, swollen, at first covered by a peridium which at maturity splits longitudinally exposing the semi-agglutinated to powdery, dark spore mass. Spores single, in pairs, or in indefinite, loose, few-spored balls. Sterile cells lacking. Spore germination: Two-celled basidia produce large, dikaryotic basidiospores, dikaryotic hyphae, or both, usually one per basidial cell, either laterally or one laterally and one terminally. Host-parasite interaction by haustoria. Septal pore simple, with membrane caps and two non-membranous plates closing the pore.

Ustacystis is currently a unispecific genus in the Urocystidaceae, treated by Vánky 2009c. Type of the genus:

Ustacystis waldsteiniae (C.H. Peck) G.L. Zundel,

Mycologia 37:796, 1945.

Urocystis waldsteiniae Peck, Annual Rep. New York State Mus. 46:112, 1893. — Ustilago waldsteiniae (Peck) Pazschke, in Rbh., Fgi. eur. no. 4011, 1895. — Tuburcinia waldsteiniae (Peck) Liro, Ann. Univ. Fenn. Abo., Ser. A, 1:90, 1922. — Whetzelia waldsteiniae (Peck) Zundel, Mycologia 37:372, 1945. — Type on Waldsteinia fragarioides, USA, New York, Albany Co., Alcove, VI.1892, leg. C.L. Shear; isotypes in Ellis & Ev., N. Amer. fgi. no. 2983, HUV 9075!, in Shear, N.Y. fgi. no. 86, HUV 5222!, and in Ellis & Ev., Fgi. Columb. no. 137, HUV 16157!

Urocystis gei Ellis & Everhart, Bull. Torrey Bot. Club 27:572, 1900. — Ustacystis gei (Ellis & Everh.) Zogg, Cryptogamica Helvetica 16:131, 1986('1985'). — Type on Geum ciliatum (= G. triflorum var. ciliatum), USA, Washington, Waitesburg, 7.V.1900, leg. R.M. Horner, 1430. (Syn. by Clinton 1902: 129).

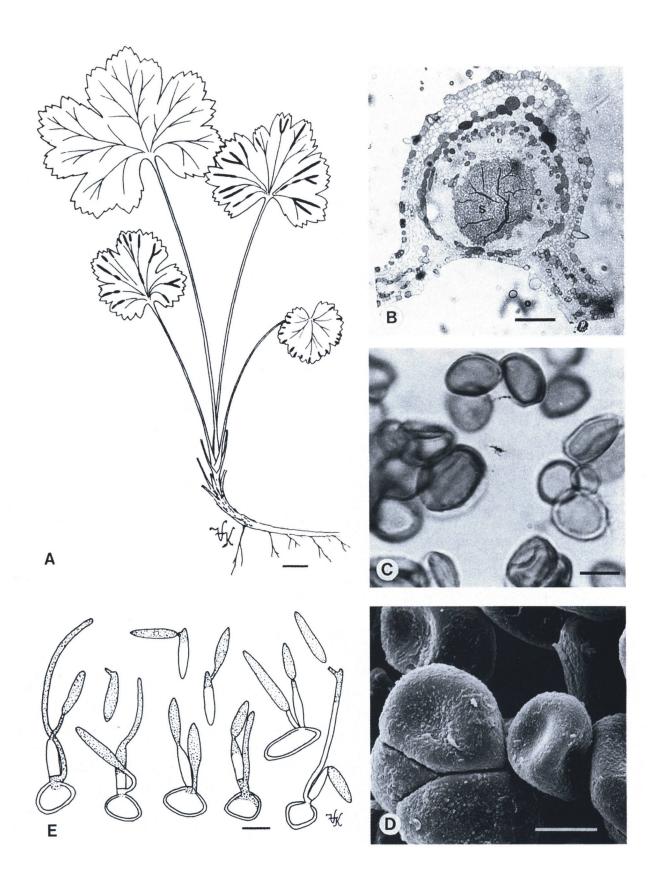
Sori (Figs. 95 A, B) in leaves, epiphyllous, following the veins, oval, linear or bifurcate, swollen, initially covered by a grayish peridium formed of host tissue, which at maturity splits longitudinally exposing the first agglutinated, later powdery, blackish or dark reddish brown spore mass. Infection systemic, appearing each season on the same plant. Infected plants flower normally. *Spores* (Figs. 95 C, D) varying in shape, size, color and wall-thickness, globose, subglobose, hemispheric, oblong or polyhedral to rather irregular, 7-12(-15) × 9-15(-18) μm, single, in pairs or adherent in groups of 3 or more, forming loose spore balls, reddish brown, with sparsely situated, low, rounded, hyaline warts. *Sterile cells* absent. *Spore germination* (Fig. 95 E) results in two-celled basidia (occasionally two, one-celled basidia per spore) producing basidiospores, hyphae, or both, usually one per basidial cell, either laterally or one laterally and one terminally. Basidiospores long-ellipsoidal or subfusiform, very large, measuring 3.5-4.5 × 24-32 μm, hyaline. They have never been observed to bud, but germinate from one or both ends, or occasionally from the side. The haplophase has been almost eliminated; basidial cells and subsequent vegetative development being dikaryotic (Hanson & Atkinson 1938).

On Rosaceae: Geum triflorum Pursh (Sieversia triflora (Pursh) R.Br.), G. triflorum var. ciliatum (Pursh) Fassett (G. ciliatum Pursh), Waldsteinia fragarioides (Michx.) Tratt., W. geoides Willd., W. ternata (Steph.) Fritsch (W. sibirica Tratt.); Europe (Hungary, Germany, Romania), E. Asia (Japan), N. America (Canada, USA).

Ref.: Hanson & Atkinson 1938, Zundel 1945a, 1945b, Ingold 1992, Bauer, Mendgen & Oberwinkler 1995a, 1995b, Vánky 2009c.

Fig. 95 A-E. Ustacystis waldsteiniae on Waldsteinia geoides, Vánky, Ust. exs. no. 629, HUV 13302.

- A. Sori on the upper, adaxial side of the leaves. Habit (Bar = 1 cm).
- **B.** T.S. of a sorus with intravascular spore mass (s) (Bar = $100 \mu m$).
- C, D. Spores in LM and in SEM (Bars = $10 \mu m$).
- E. Spore germination (on WA, at room temp., in 2-6 days; Bar = $10 \mu m$).



96. USTANCIOSPORIUM K. Vánky,

Mycotaxon 70:31, 1999; emend. Piepenbring, Nova Hedwigia 70:330, 2000.

GYMNOCINTRACTIA M. Piepenbring, D. Begerow & F. Oberwinkler, Mycologia 91:496, post 4.III.1999. — Type: G. montagnei (Tul. & C. Tul.) M. Piepenbr., Begerow & Oberw. on "Schoenus sp." (= Rhynchospora rugosa (Vahl) Gale), Algeria.

Sori in spikelets of plants in Cyperaceae, surrounding the tip of the axis of sterile flowers, filling them with a black, initially agglutinated, later powdery mass of spores. Sterile fungal stroma and peridium lacking. Spores single or in balls, pigmented (yellowish or reddish brown), slightly flattened, often with a hyaline appendage; spore wall uneven, ornamented (foveolate). Spore germination results in phragmobasidia whose basidial cells form basidiospores or conjugate. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Ustanciosporium, tentatively classified in the Anthracoideaceae, has 20 recognized species on host plants in seven genera of Cyperaceae (Bulbostylis, Cyperus, Fimbristylis, Rhynchospora, Rikliella, Scirpus, Scleria). It contains species with single spores and with spore balls. Type of the genus:

Ustanciosporium rhynchosporae K. Vánky,

Mycotaxon 70:31, 1999.

Type on *Rhynchospora rugosa*, South Africa, KwaZulu-Natal Prov., Drakensberg Mts., Loteni Nature Reserve, 1 km W of Camp site, alt. c. 1620 m, 6.I.1997, leg. C. & K. Vánky. — Holotype HUV 1840!; isotypi in PREM, BPI et in Vánky, Ust. exs. no. 1042.

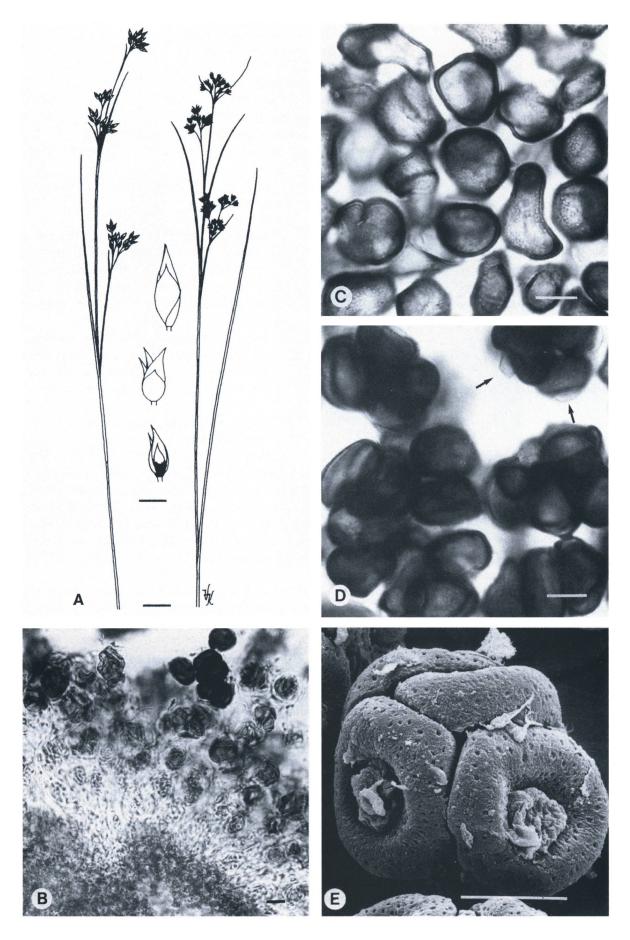
Sori (Figs. 96 A, B) in the spikelets completely hidden by the outermost glumes, filled with a black, granular-powdery mass of spore balls. The basal part of the sori is formed of host tissues of the more or less destroyed inner floral organs, permeated by hyphae. On the surface of the host tissues, the sporogenous hyphae concentrate into small groups from which spore balls develop (Fig. 96 B). The proper sorus is a globoid, black, agglutinated body of 1-2 mm diameter, with mature, granular-powdery spore balls on its surface. Infection systemic. Infected plants slightly stunted having somewhat smaller and congested flowers. *Spore balls* (Figs. 96 D, E) subglobose, ovoid, elongate, usually more or less irregular, 15-40 x 25-55(-70) μm, reddish brown, composed of 2-25 (or more?, mostly of 3-9) spores, by pressure separating into single spores. *Spores* (Figs. 96 C, D, E) extremely irregular, rounded, subpolyhedrally irregular, elongate, curved, often with 1(-3) subacute or acute points and a flattened or depressed side, where a short, hyaline appendage may be present, 10-16(-18) x 14-22(-25) μm, reddish brown; wall uneven, 1-1.5 μm, at the points up to 3 μm thick, finely, rather sparsely, regularly foveolate. *Spore germination* is not known.

On Cyperaceae: *Rhynchospora rugosa* (Vahl) S. Gale (*R. brownii* Roem. & Schult.; *R. glauca* Vahl); S Africa (South Africa). Known only from the type collection.

Ref.: Liro 1938, Ling 1950b, Vánky 1999a, Piepenbring, Begerow & Oberwinkler 1999, Piepenbring 2000.

Fig. 96 A-E. Ustanciosporium rhynchosporae on Rhynchospora rugosa, holotype, HUV 18400.

- **A.** Sori in the spikelets. A healthy inflorescence (left), and a diseased inflorescence (right). Habit (Bar = 1 cm). Enlarged a healthy (top) and two infected spikelets (Bar = 1 mm).
- **B.** T.S. of a young sorus, showing the development of the spore balls (Bar = $10 \mu m$).
- C, D, E. Spore balls and spores in LM and in SEM. In D. the arrows show the hyaline appendage of the spores (Bars = $10 \mu m$).



97. USTILAGO (C.H. Persoon) H.F.A. Roussel,

Flore du Calvados, Ed. 2:47, 1806.

NECROSIS Paulet, Traité Champ. I:548, 1793 (n.v.; fide Dietel, 1928:7).

UREDO subgen. USTILAGO Persoon, Syn. meth. fung. 1:224, 1801.

PERICOELIUM Bonorden, Handb. Allgem. mycol. (Stuttgart):44, 1851 (n.v.).

USTILAGIDIUM Herzberg, in Zopf, Beitr. Physiol. Morph. Nieder. Organ., 5:7, 1895 (n.v.).

MYCOSARCOMA Brefeld, Unters. Gesammtgeb. Mykol. 15:53, 1912 (nom. nud.). — Type: M. maydis (DC.) Bref. (= Ustilago maydis (DC.) Corda) on Zea mays L., Europe.

YENIA Liou, Contr. Inst. Bot. Natl. Acad. Peiping 6:43, 1949. — Type: Y. esculenta (Henn.) Liou on Zizania latifolia (Griseb.) Turcz. ex Stapf, N Vietnam (= Ustilago esculenta Henn.).

Sori in various parts of host plants in Poaceae, at maturity bursting and exposing usually powdery, sometimes agglutinated, blackish, or olive-brown spore mass. Sterile cells absent. Spores single, small to medium-sized, pigmented (brown, without violet tint), usually ornamented (verruculose, echinulate or irregularly verrucose-reticulate, etc.), rarely smooth. Spore germination results in phragmobasidia bearing lateral and apical basidiospores or hyphae. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless.

Ustilago is the type genus of the Ustilaginaceae. It has c. 200 known species parasitizing members of the Poaceae. The limits between Ustilago, Sporisorium s. lat. and Macalpinomyces are not sharp, with many intermediate species. The complex was divided recently by McTaggart et al. (2012c) into Anthracocystis, Langdonia, Macalpinomyces, Sporisorium s. str., Stollia, Triodiomyces and Ustilago. Type of the genus:

Ustilago hordei (C.H. Persoon: C.H. Persoon) G. Lagerheim, nom. cons. Mitt. Bad. Bot. Vereins 1889:70, III.1889.

as "Ustilago hordei (Rabenhorst)"; non Ustilago hordei Brefeld 1888:1593, q.e. U. tritici, and nomen ambiguum. — Uredo segetum Pers. α hordei Persoon, Tent. disp. method. fung.:57, 1797. — Uredo segetum Pers. α Uredo hordei Pers.: Persoon, Syn. meth. fung. 1:224, 1801. — Uredo carbo DC. α hordei (Pers.: Pers.) De Candolle, Fl. franç., ed. 3, 6:76, 1815. — Erysibe vera Wallr. α. hordei (Pers.: Pers.) Wallroth, Flora Cryptogamica Germaniae, Sect. 2, 4:217, 1833. — Ustilago segetum (Pers.) Roussel var. hordei (Pers.: Pers.) Rabenhorst, in Rbh., Herb. viv. myc. ed. 2, no. 397, 1856. — Ustilago segetum (Pers.) Roussel var. hordei (Pers.: Pers.) Brunaud, Actes Soc. Linn. Bordeaux, Sér. 4, 2:163, 1878 (comb. superfl.). — Type on Hordeum [distichon vel vulgare], Europe (comp. Mortensen, Rostrup & Ravn 1908:148, Lind 1913:258).

For taxonomic synonyms, such as *Reticularia segetum* Bull., *Ustilago segetum* var. *hordei* ("Hordii") forma tecta Rostr. & Jensen, *U. avenae* (Pers.: Pers.) Rostr. var. *levis* Kellerman & Swingle, *U. kolleri* Wille, *U. dura* Appel & Gassner, *U. arrhenatheri* Schellenb., *U. rostrupii* Kitunen, and their literature, see Vánky, *Smut Fungi* of the World, 2011('2012'):1209-1210.

Sori (Fig. 97 A) in all spikelets of an inflorescence as a blackish brown, adherent spore mass, at first covered by a membrane of host tissue origin ("covered smut"), later exposed to various degrees depending on the extent of destruction of the spikelet parts. Spores (Figs. 97 B, C) globose, subglobose to ovoid, 5-9(-10) μm in diameter, paler colored on one side, smooth. Spore germination (Fig. 97 D) results in a four-celled basidium (often of the 3 + 1 pattern, where the 4th cell remains in the spore) on which ovoid basidiospores are produced on artificial media. Dikaryons, formed between either compatible basidial cells or basidiospores, infect seedlings.

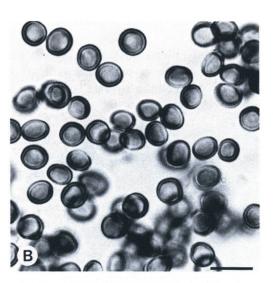
On Poaceae: Arrhenatherum, Avena, Elymus, Hordeum species; cosmopolitan.

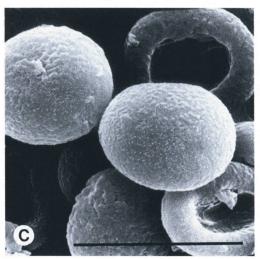
Ref.: Ciferri 1953, Nannfeldt in Lindeberg 1959, Huang & Nielsen 1984, Schmitter 1984, Nielsen 1993.

Fig. 97 A-C. Ustilago hordei on Hordeum vulgare, Vánky, Ust. exs. no. 86, HUV 3776.

A. An infected spike with sori of the covered smut of barley. Habit. **B, C.** Spores in LM and in SEM. In C. the thin-walled part of the dry spores has collapsed (Bars = $10 \mu m$). **D.** Spore germination (after Jørgensen 1963('1962'):99).









D

98. USTILENTYLOMA D.B.O. Savile,

in Savile & Parmelee, Canad. J. Bot. 42:708, 1964.

Sori as spots on leaves of host plants in Poaceae. Spores single, in loose or compact groups, embedded in the host tissue, not powdery, subhyaline or pale yellow. Resembles Entyloma but germination of Ustilago-type. Host-parasite interaction by intercellular hyphae lacking interactions with deposits of specific fungal vesicles. Septa with simple pores lacking caps.

Ustilentyloma belongs to the Ustilentylomataceae within the order Microbotryales. Savile separated this genus from the morphologically similar *Entyloma* on the basis of the phragmobasidial spore germination; in *Entyloma* this is of holobasidial type. The differences in spore germination of these two genera reflect their phylogeny as supported also by ultrastructural and molecular studies. Four species of *Ustilentyloma* are known:

1. U. brefeldii (Krieger) Vánky, on Agropyron, Arrhenatherum, Calamagrostis, Elymus, Festuca, Holcus, Leymus, Phalaris, and Poa species, in Europe,

2. U. fluitans (Liro) Vánky, on Glyceria species, in Europe,

3. U. oreochloae (Durrieu) Vánky, on Oreochloa from France, and 4. The type of the genus:

Ustilentyloma pleuropogonis D.B.O. Savile,

in Savile & Parmelee, Canad. J. Bot. 42:708, 1964.

Type on *Pleuropogon sabinei*, Canada, Franklin Distr., Queen Elisabeth Islands, Ellef Ringnes Island, 2.4 km SW of Isachsen, 15.VII.1960, leg. D.B.O. Savile 4247F, DAOM 92912.

Sori in leaves forming small, elongate, scattered, yellowish brown spots. Spores embedded in the host tissue, mostly gregarious, globose, or polyangular by mutual pressure, 9-14.5 x 11.5-19(-21) μ m, with hyaline, smooth, 0.4-0.8 μ m thick wall. Spore germination results in a 4-celled, hyaline basidium, 5-6.5 x 23-30 μ m, on which sessile basidiospores are produced laterally; basidiospores ovoid, thin-walled, hyaline, 3-3.5 x 6.5-8 μ m (Savile & Parmelee 1964:708).

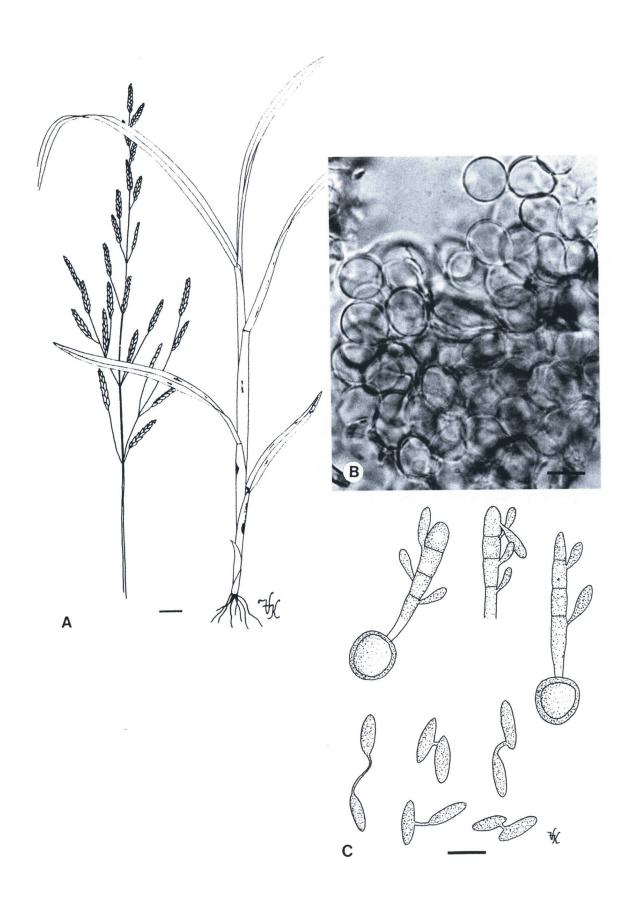
On Poaceae: Pleuropogon sabinei R.Br.; N America (Canada).

Ref.: Savile & Parmelee 1964, Vánky 1970, 2001c, Denchey 1995.

This genus is illustrated by *Ustilentyloma fluitans*.

Fig. 98 A-C. *Ustilentyloma fluitans* (Liro) Vánky on *Glyceria fluitans* (L.) R.Br., Vánky, Ust. exs. no. 500, HUV 11564, and on *G. plicata* Fr., Vánky, Ust. exs. no. 80, HUV 5205.

- **A.** Sori on leaves and leaf sheaths of G. plicata. Habit (Bar = 1 cm).
- **B.** Spores on G. fluitans in LM (Bar = $10 \mu m$).
- C. Spore germination (in situ) on G. plicata. Haploid basidiospores conjugate in pairs by conjugation bridges, to initiate the parasitic dikaryophase (not shown; (Bar = $10 \mu m$).



99. VANKYA D. Ershad, s. str.

Rostaniha 1:66, 2000.

Sori on leaves of plants in Liliaceae s. str., forming pustules or swellings, filled with blackish brown, powdery spore mass, lacking peridium and columella. Spores single, olive-brown, without violet tint or pale yellow, orange or rusty color. Sterile cells present between the spores, indistinct. Spore germination results in phragmobasidia. Host-parasite interaction by haustoria. Septal pore simple with two membrane caps and two non-membranous plates closing the pore. Type: V. ornithogali.

Ershad (2000:66) described the genus *Vankya*, for "*Ustilago*" species on Liliaceae, with three species: **1.** *V. ornithogali* (J.C. Schmidt & Kunze) Ershad on *Gagea* species, **2.** *V. heufleri* (Fuckel) Ershad, on *Erythronium* and *Tulipa* species, and **3.** *V. vaillantii* (Tul. & C. Tul.) Ershad, on *Albuca, Bellevalia, Chionodoxa, Eucomis, Hyacinthus, Muscari, Puschkinia, Scilla* and *Urginea* species. Bauer *et al.* (2008) demonstrated that this third species, in the anthers of members of Hyacinthaceae, belongs to another genus, for which *Antherospora* was proposed, including several species. Vánky (2009b) demonstrated that *V. ornithogali* occurs only on species of *Gagea*, and sterile cells are present between the spores. A third species of *Vankya*, *V. lloydiae* Vánky, on *Lloydia* from E Asia (Russia) was also described. *Vankya* belongs to the Urocystidaceae. *Type of the genus:*

Vankya ornithogali (J.C. Schmidt & G. Kunze) D. Ershad, Rostaniha 1:66, 2000.

For nomenclatural and taxonomic synonyms, such as *Uredo ornithogali* J.C. Schmidt & Kunze, *Ustilago ornithogali* (J.C. Schmidt & Kunze) Kühn, *Ustilago ornithogali* (J.C. Schmidt & Kunze) Magnus on *Gagea* cf. *lutea*, as well as *Caeoma ornithogali* Schltdl. on *Gagea* cf. *pratensis*, *Ustilago ornithogali* J. Schröter on *Gagea minima*, *Ustilago umbrina* J. Schröter on *Gagea pratensis*, and *Ustilago heterospora* Niessl on *Gagea bohemica*, see Vánky, *Smut Fungi of the World*, 2011('2012'):1309-1310.

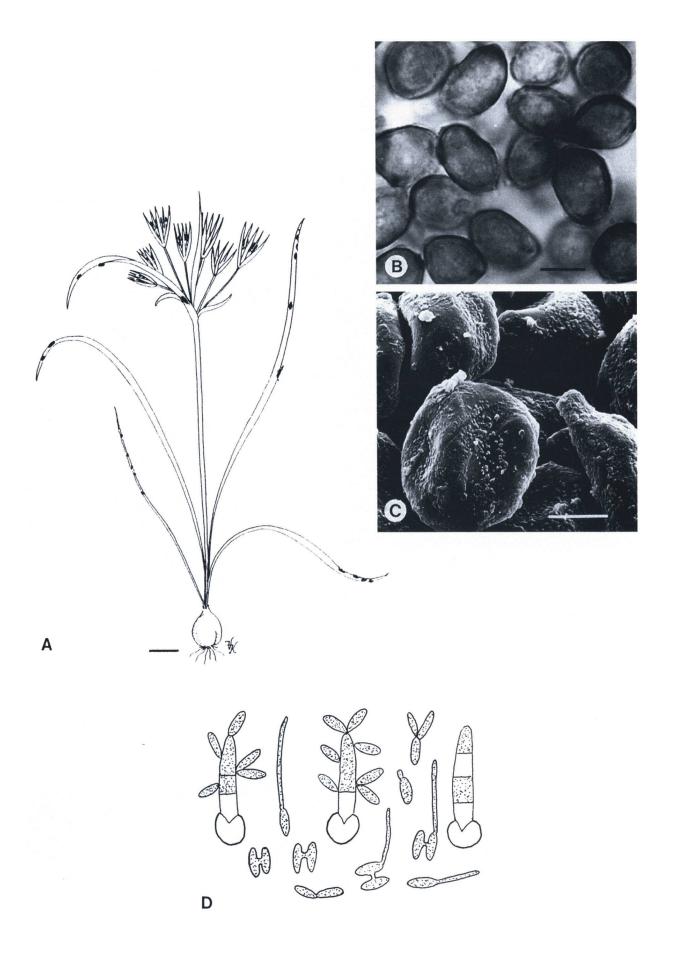
Sori (Fig. 99 A) in leaves and bracts forming 1-5(-10) mm long, ellipsoidal or fusiform pustules, initially covered by the epidermis, which ruptures longitudinally to expose the blackish brown, powdery spore mass. Infection systemic, appearing year after year on the same host plant. Spores (Figs. 99 B, C) varying in shape and size, subglobose, ovoid, irregular, subpolyhedral or elongate, not rarely with an acute tip, sometimes with a short pedicel, 9.5-15 x 10.5-19(-24) μm, yellowish to reddish brown; wall 0.5-1.5 μm thick, apparently one-layered, nearly smooth to finely, rather densely punctate-verruculose, the dots not affecting the spore profile. Sterile cells few, solitary or in groups of 2-4, subglobose, ellipsoidal, slightly irregular, rarely elongated, collapsed in old specimens, 11-20 μm long, usually of the same color as the spores; wall 1.5-3(-4) μm thick, one-layered, smooth, in SEM, at high magnification, rough. Spore germination (Fig. 99 D) results in phragmobasidia on which ovoid to short ellipsoidal, sessile basidiospores are produced laterally and terminally. Basidiospores may conjugate giving rise to dikaryotic hyphae or they bud forming yeast colonies (Cocconi 1889). Sterile cells few, solitary or in groups of 2-4, subglobose, ellipsoidal, slightly irregular, rarely elongate, collapsed in old specimens, 11-20 μm long, usually of the same color as the spores; wall 1.5-3(-4) μm thick, one-layered, smooth.

On Liliaceae s. str.: At least on 27 species of Gagea; Europe, N Africa, Asia.

Ref.: Cocconi 1889, Schellenberg 1911, Liro 1924, Ershad 2000, Bauer, Lutz, Begerow, Piątek, Vánky, Bacigálova & Oberwinkler 2008, Vánky 2009b.

Fig. 99 A-D. Vankya ornithogali on Gagea spp.

- **A.** Sori on the leaves and bracts of *Gagea arvensis* (Pers.) Dumort. Habit. Vánky, Ust. exs. no. 437 (as *Ustilago ornithogali*; (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM, on *Gagea* cf. *lutea* (L.) Ker.-Gawler, isotype, HUV 13280 (Bars = 10 μm).
- **D.** Germinating spores from *G. arvensis* on nutrient media (after Cocconi 1889, fig. 3).



100. *WEBSDANEA* K. Vánky, *Mycotaxon* 65:184, 1997.

Sori in vegetative tissues of host plants in Restionaceae, filled with spore balls, bursting at maturity. Spore balls composed of spores only, differentiated within a sporogenous mass of hyphae. Peridium, columella and sterile cells lacking. Spores pigmented (brown, without violet or orange-yellow tint). Spore germination results in septate basidia on which basidiospores on sterigmata or also hyphae are produced. Host-parasite interaction by intracellular hyphae, coated by an electron-opaque matrix. Mature septa poreless. Parasitic hyphae inter- and intracellular. Type of the genus: W. lyginiae.

Websdanea is a unispecific genus in the Websdaneaceae within the order Ustilaginales.

Websdanea lyginiae (K.A. Websdane, K. Sivasithamparam, K.W. Dixon & J.S. Pate) K. Vánky, Mycotaxon 65:184, 1997.

Ustilago lyginiae Websdane, Sivasithamparam, K.W. Dixon & Pate, *Mycotaxon* 48:485, 1993. — Type on *Lyginia barbata*, Australia, Western Australia, Perth, Gosnells suburb, 16.IV.1992, leg. J.S. Pate, PERTH; isotype in Herb. Kings Park, Perth.

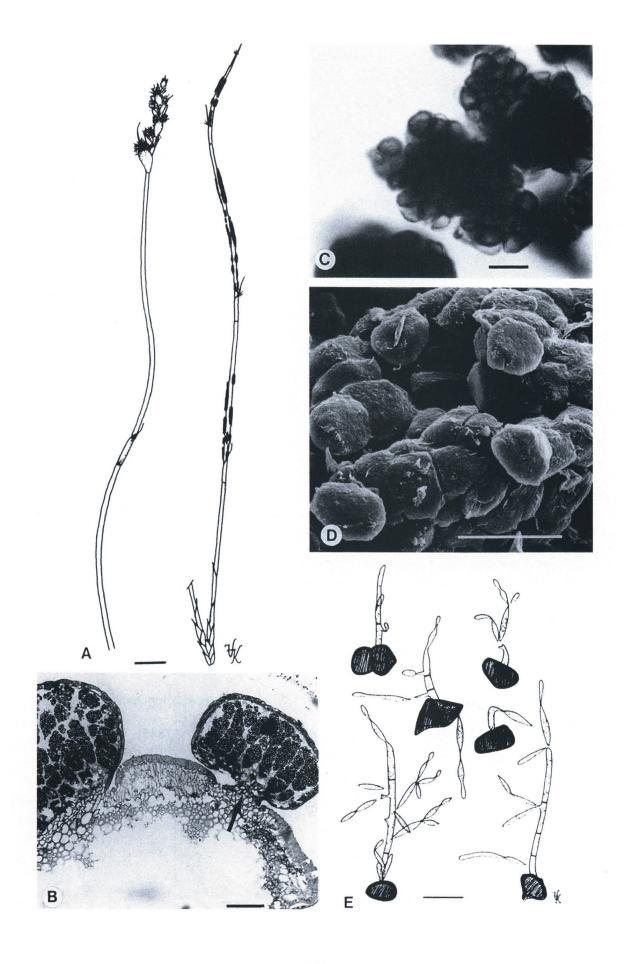
Sori (Figs. 100 A, B) as bullate, dark reddish brown striae on the distal internodes of the culms, c. 1 x 1-50 mm, covered by the epidermis which ruptures at maturity disclosing the black, granular-powdery mass of irregular, loose spore balls. The swollen sori develop in longitudinal depressions of the culm, starting from a more or less narrow isthmus composed of sporogenous hyphae and host cells permeated by inter- and intracellular hyphae. In young sori, within the basal, sporogenous hyphae, groups of spore balls differentiate and during maturation are pushed toward the periphery. When young, the groups of spore balls are separated into irregular lobes by fascicles of sporogenous hyphae which penetrate into the sori. During maturation, these fascicles disappear towards the periphery. Infection systemic; usually all culms of a plant are affected. Smutted culms are sterile. Spore balls (Figs. 100 B, C, D) varying in shape and size, subglobose, ovoid to usually irregularly elongate, 30-90 x 45-200 μm, dark olive-brown, opaque, composed of many, easily separating spores. Spores (Figs. 100 C, D, E) extremely varying in shape and size, subglobose, ovoid, irregularly subpolyhedral or polyhedral, elongate, often prolonged into one or two shorter or longer, subacute or acute tips, (5-)6-9 x (6-)7-13(-16) μm, olive-brown; wall unevenly thick, 0.5-1.5 μm, in LM smooth, in SEM outer spores inconspicuously low verruculose, inner spores smooth. Spore germination (Fig. 100 E) results in (1-)2-4-celled basidia, c. 1.5 x (6-)20-40 μm. On the basidia, on well-developed sterigmata, fusiform or ovoid basidiospores are produced successively, 1-1.5 x 3.5-12 μm. The basidiospores bud giving rise to smaller, fusiform or ovoid cells or hyphae. In other cases, on the basidia abundantly ramifying hyphae are produced and only a few ovoid basidiospores on the top of shorter or longer branches.

On Lyginiaceae (Restionaceae s. lat.): Lyginia barbata R.Br.; Australia.

Ref.: Websdane, Sivasithamparam, Dixon & Pate 1993, Vánky 1997f, 2006a.

Fig. 100 A-E. Websdanea lyginiae on Lyginia barbata, Vánky, Ust. exs. no. 996 (as Ustilago lyginiae), HUV 17900.

- A. Sori producing bullate striae on the sterile stem. Habit. Healthy, flowering shoot (left) (Bar = 1 cm).
- **B.** T.S. of a culm with sori, with the narrow isthmus (arrow) between the stem and the sorus filled with spore balls (Bar = $100 \mu m$).
- C, D. Spore balls and spores in LM and in SEM (Bars = $10 \mu m$).
- **E.** Germinating spores (on WA, at room temp., in 2 days). Fusiform or ovoid basidiospores are produced on sterigmata on the basidia, laterally and terminally (Bar = $10 \mu m$).



101. *YELSEMIA* J. Walker, *Mycol. Res. 105*:225, 2001.

Sori in various parts of dicotyledonous host plants, swollen, bursting at maturity exposing a black, powdery mass of spores. Columella and sterile cells lacking. Spores single, dark pigmented (brown) without violet tint, each spore with two oppositely situated, pale-colored polar caps. Spore germination, through the polar caps, results in holobasidia on which apically several hyaline, septate, broadly fusiform basidiospores are produced which give rise to hyphae. Host-parasite interaction by haustoria. Septal pore simple, with membrane caps, no inner plates.

Yelsemia, on both monocotyledonous (Anthericaceae, Liliaceae s. lat.) and dicotyledonous (Byblidaceae, Campanulaceae, Droseraceae) host plants, belongs to the Melanotaeniaceae within the order Urocystidales. It is a genus of four known species: 1. Y. droserae R.G. Shivas, Vánky & Athipunyakom, on Drosera species, from Thailand and Australia, 2. Y. lowrieana R.G. Shivas & Vánky, on Byblis rorida Lowrie & Conran, from Australia, 3. Y. speculariae (Stevenson) Vánky & Bauer, on Specularia perfoliata (L.) DC., from USA, and 4. The type of the genus:

Yelsemia arthropodii J. Walker,

Mycol. Res. 105:227, 2001.

Type on *Arthropodium minus*, Australia, New South Wales, 25 km NE of Griffith, Cocoparra National Park, 14.IV.1990, leg. P.A. McGee, DAR 63312; isotypes (from artificial infection) DAR 65774, HUV 18451!

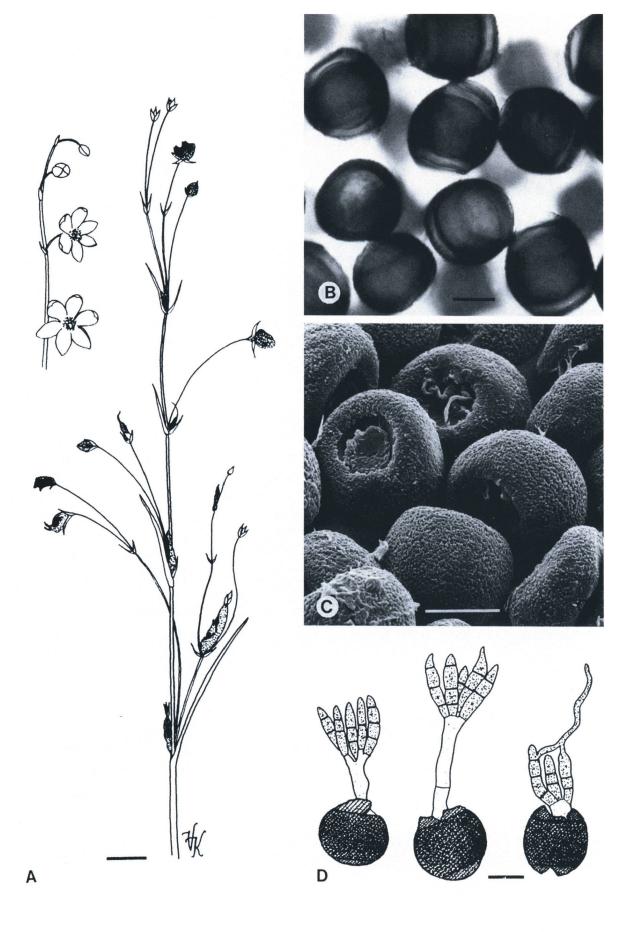
Sori (Fig. 101 A) in stems, leaf axils and seeds, swollen, more or less distorting the host organs, leaden to grayish black, 3-5 x 6-8(-20) mm. Mature sori burst, exposing a black, granular-powdery mass of spores. Columella and sterile cells lacking. Spores (Figs. 101 B, C, D) single, globose, subglobose to ovoid, 16-22 × 20-25 μ m, with a 12-18 μ m wide, dark blackish brown equatorial band and two oppositely situated, hyaline to pale brown polar caps, 3-6.5 μ m high, 12-15 μ m wide. The polar caps are results of the separation of the inner and outer layers of the spore wall in these areas, the space between them being filled with a homogeneous, transparent substance. Spore wall of the equatorial part 2-2.5 μ m thick, finely, densely verruculose; wall beneath the polar caps thinner, paler colored, smooth. The outer wall at the polar areas is thin, pale yellowish brown, minutely verruculose. Infection in seedling stage, systemic, results in production of several flowers per node and elongation of sterile bracts and floral pedicels. Spore germination (Fig. 101 D), through the polar caps, results in one or two aerial holobasidia, from very short to 50 μ m long, at the base 4-6 μ m wide, at the apex 9-10 μ m wide, sometimes with two branches near the apex. Mature basidia usually with 1-3 retraction septae, and 2-6 apical, broadly fusiform, hyaline basidiospores 4-6 x 25-50 μ m, initially unicellular, later with 1-3(-4) transverse septa and germinating from one or several cells by 1-2 hyphae, often forming anastomoses with neighboring basidial cells to produce dikaryotic infection hyphae (Walker, 2001:227).

On Anthericaceae (Liliaceae s. lat.): Arthropodium curvipes S. Moore, A. minus R.Br.; Australia.

Ref.: Walker 2001, Vánky 2002b, Shivas & Vánky 2003, Vánky, Shivas & Athipunyakom 2006.

Fig. 101 A-D. Yelsemia arthropodii on Arthropodium minus, isotype, HUV 18451.

- A. Sori producing swellings on the stems, leaf axils and seeds. Healthy flowers (left). Habit (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM. Note the paler polar caps on the LM picture, which appear as rounded, collapsed areas in C (Bars = $10 \mu m$).
- **D.** Germinating spores (on Potato Dextrose Agar, at room temp., in 5 days; drawings kindly supplied by John Walker; comp. also Walker, 2001:230, Figs. 16, 17).



102. ZUNDELIOMYCES K. Vánky,

Trans. Brit. Mycol. Soc. 89:477, 1987.

Sori as locular galls with central cavities and longitudinal septa formed of host tissue and hyphae on host plants in Polygonaceae (*Polygonum*), covered by a thick peridium of host origin permeated by hyphae. Columella lacking. Spore masses lining the cavities, semi-agglutinated, pale-colored. Spores hyaline, of two kinds: central, thin-walled, single spores, and peripheral, thick-walled, agglutinated ones. Host-parasite interaction by intercellular hyphae lacking interactions with deposits of specific fungal vesicles. Mature septa poreless.

Zundeliomyces is a unispecific genus in the Microbotryaceae (Microbotryales, Urediniomycetes). Type of the genus:

Zundeliomyces polygoni K. Vánky,

Trans. Brit. Mycol. Soc. 89:477, 1987.

Type on *Polygonum alpinum*, Kazakhstan, Alma Ata Region, Dzhungarskij Alatau Mt., on the top of a stony slope near the village of Sarkand, alt. c. 1300 m, 27.VI.1955, leg. V.M. Mihailova, HUV 12646!; isotypes in AA, BP, BPI, K, LE.

Sori (Figs. 102 A, B) in scattered flowers as conspicuous, 3(-5)-lobed swellings, 6-10 mm in diameter, comprising all the essential parts of the flowers although the distal part of the more or less aborted nuts, sometimes also the perianth and exceptionally a few filaments may be left intact. A permanent, rather thick peridium of host tissue permeated by hyphae encloses the semi-agglutinated, pale ochre- or butter-colored mass of spores. Each sorus-lobe contains one or more large cavities and longitudinal septa of host tissue and fungus origin. Columella lacking. Spores (Figs. 102 B, C, D) hyaline, of two kinds: 1) solitary or loosely connected, thin-walled, usually ellipsoidal, ridged; these spores are centrally situated in the sorus-lobes, lining the cavities, and 2) thick-walled, globose, tuberculate, agglutinated spores, connected by several thick, gelatinous processes; these spores are situated peripherally, between the peridium and the thin-walled spores. The spores of the first type are (subglobose-) elliptical to lemon-shaped, 7-9 x 8-11 µm, wall c. 1 µm thick, with rather densely situated, longitudinal ridges separated by alternating deep and shallow furrows, barely visible in LM, but evident in SEM, along with weak transversal connections between the ridges. In LM, in stained spores, the deep furrows appear as "interruptions" in the exospore when the spores are viewed parallel to their long axis. In TEM the spore wall is two-layered: the inner layer is compact, c. 0.3 µm thick. Long ridges (in T.S. appearing as spines) penetrate from the inner layer into the variably thickened (0.1-0.5 μm) outer layer, which has a loose, wavy, fibrillar structure. The spores of the second type are globose, varying in size, 9-15 μm in diameter, often possessing a slightly uneven, (1-)1.5-3 μm thick wall, in LM with a few large, but low, tubercles (remnants of the processes), in SEM, in addition, with numerous small tubercles; in TEM the wall is two-layered, structurally similar to the first type of spores but both layers are considerably thicker (both measuring 0.6-0.8 µm in diameter without the tubercles), lacking ridges or spines. Spore germination is not known.

On Polygonaceae: *Polygonum alpinum* All.; Asia. Known only from the type locality.

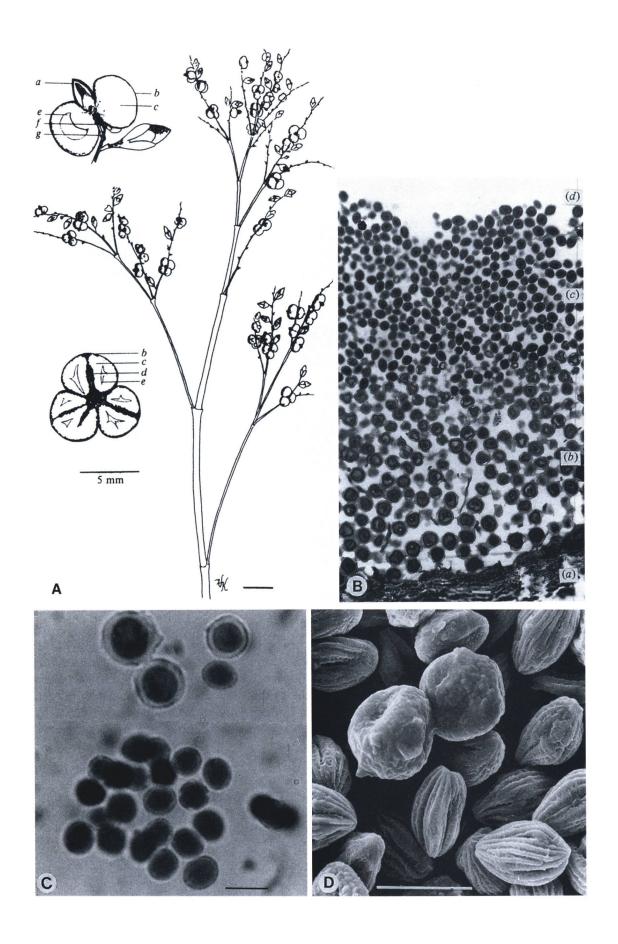
Ref.: Vánky 1987c.

Fig. 102 A-D. Zundeliomyces polygoni on Polygonum alpinum, holotype, HUV 12646.

A. Sori in some flowers of the inflorescence. Habit (Bar = 1 cm). Enlarged a pair of a healthy flower and a L.S. of a sorus (top left) and a T.S. (below) of a sorus with (a) partly aborted nut, (b) peridium, (c) spore mass, (d) septum, (e) cavity, (f) pedicel, (g) perianth (Bar for the detail drawings = 5 mm).

B. T.S. of a part of a sorus in LM, stained with crystal violet. (a) sorus membrane, (b) the layer of the thick-walled, globose spores, connected with each-other, (c) the inner layer of the thin-walled, ellipsoidal, more or less solitary spores, and (d) the central cavity.

C, D. Spores in LM (stained with cotton blue in lactophenol) and in SEM (Bars = $10 \mu m$).



ASCOMYCETOUS GENERA

103. *RESTILAGO* K. Vánky, *Mycol. Balcan. 5*:70, 2008.

Sori around the fruits of plants in Restionaceae, composed of a white, basal stroma of host and fungus origin. On the stroma black, hard, firmly agglutinated, non-pulverulent spore masses are produced. Peridium, columella and sterile cells lacking. Spores single, dark pigmented (brown), ornamented, agglutinated by the outermost, gelatinous layer of the spore wall. Septal pore simple, associated with Woronin bodies. Spore germination results in simple or ramified hyphae. Type of the genus: R. capensis.

Restilago is an ascomycetous genus of unknown affinity. Around its simple septal pores there are Woronin bodies (Fig. 7, pg. 20), typical for filamentous Ascomycota. This fungus belongs to the smut fungi, because it has a similar plant parasitic life strategy and it produces thick-walled, pigmented spores (similar to the teliospores of basidiomyceteous smut fungi), which germinate to infect new plants.

Restilago capensis K. Vánky, Mycol. Balcan. 5:70, 2008.

Type on *Ischyrolepis capensis*, South Africa, Western Cape Province, Cape Town, Table Mountain, above Kirstenbosch Botanical Garden, Nursery Ravine, alt. c. 700 m, 9.XII.1996, leg. C. & K. Vánky, HUV 18033!; isotype in PREM. Paratype: Western Cape Province, Swartberg Pass, between Oudtshoorn and Prince Albert, alt. c. 1130 m, 17.XII.1996, leg. C. & K. Vánky, HUV 18036!

Sori (Figs. 103 A, B) around some of the capsules of an inflorescence forming black, globoid or flattened, 'heart-shaped', hard, non-pulverulent bodies, c. 2-3 mm high, 2-3 × 3-4 mm wide. Distal part of the sori 2- or 4-lobed according to the apical part of the capsule, with the persistent, protruding style between the lobes. The surface of the sori is formed of a compact mass of agglutinated spores. Basal part of the sori narrowed, composed of a white stroma of sporogenous hyphae and host tissues forming pockets with spore masses at maturation (Fig. 103 C). Peridium, columella and sterile cells in the sori lacking. The sori become soft in water and release the blackish brown, floating mass of spores. *Spores* (Figs. 103 D, E) globose, ellipsoidal, ovoid to elongated, (9-)9.5-14.5 × (10-)11-20(-22) μm, dark reddish brown; wall even, c. 1 μm thick, densely verrucose, spore profile finely serrulate. A thin, hyaline, gelatinous layer is covering the spores which when dry glues the spores firmly together or to the substrate. *Spore germination* (Figs. 103 F) results in simple or ramified hyphae.

On Restionaceae: Ischyrolepis capensis (L.) H.P. Linder; South Africa. Known only from the type collections.

The biology and life cycle of *Restilago capensis* is unknown. Because only some (rarely all) fruits of an inflorescence are infected, it appears that infection is localized in the flowers, similar to *Anthracoidea* species. The hard, compact spore mass excludes a dispersal by wind. When sori are put in water, the dry, gelatinous outer layer of the spores absorbs water, swells up and after a short time spore masses are abundantly released into the water. It appears that rain-splash plays an important role in dispersal and infection of new plants, by enabling spores to fall on the stigma of some flowers of healthy plants, where they germinate and infect them.

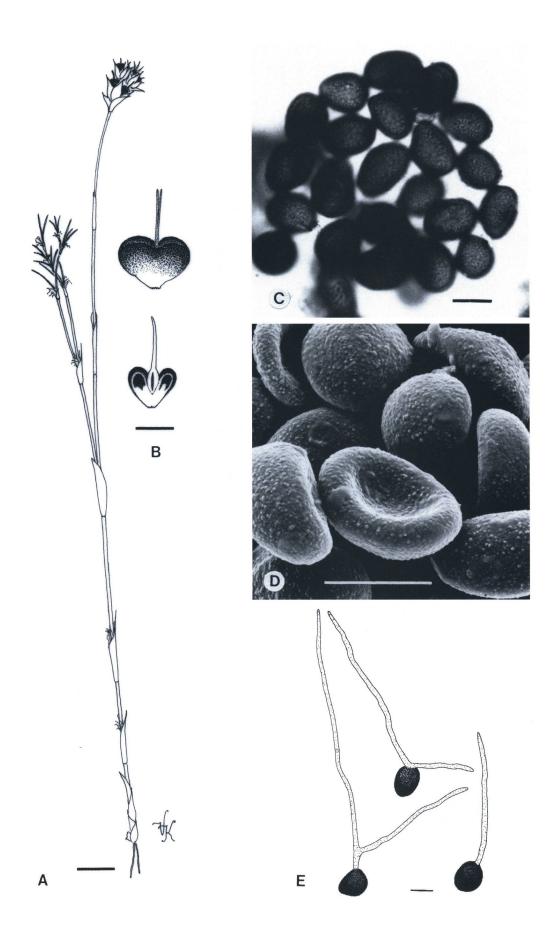
Ref.: Vánky 2008a.

Fig. 103 A-E. Restilago capensis on Ischyrolepis capensis, holotype, HUV 18036.

A, B. Sori of *Restilago capensis* around the capsules. **A.** Habit (Bar = 1 cm), **B.** enlarged two sori, one longitudinally sectioned (Bar = 2 mm).

C, D. Spores in LM and in SEM (Bars = $10 \mu m$).

E. Germinating spores (on WA, at room temp., in 2 days; Bar = $10 \mu m$).



104. SCHROETERIA G. Winter,

in Rabenhorst, Kryptogamen-Flora, etc., 2. Aufl., 1. Pilze, I. Abt.:117, 1881.

GEMINELLA J. Schröter, Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss. 1869/1872:5, 1869; Hedwigia 9:137, 1870, later homonym, non Geminella Turpin 1828 (q.e. genus Chlorophytarum, Ulotrichaceae).

Sori in seeds of Scrophulariaceae (Veronica spp.) forming a gray, grayish blue or grayish black, powdery spore mass. Infection systemic. Infected plants do not differ in appearance from healthy ones. Spores in pairs, in chains of three or more spores, sometimes single, formed by division of the spore mother cell, often easily separating into single spores. Spore germination results in short, bottle-shaped, one-celled germ tubes, and/or in long, septate, often shortly ramified germ tubes. On the top of each germ tube, or branch of germ tube, successively globose sporidia (= conidia) are produced endogenously, often in chains. Septal pore with pore plug and Woronin bodies at the septa.

The genus *Schroeteria* was studied by Vánky (1981a, 1983). There are six known species, all in the seeds of *Veronica* species. These are: **1**. *S. banatica* Vánky, **2**. *S. bornmuelleri* Magnus, **3**. *S. bremeri* Petrak, **4**. *S. decaisneana*, **5**. *S. delastrina*, and **6**. *S. poeltii* Vánky. Some species described earlier as *Schroeteria* belong to *Mycosyrinx*, which also has spores in pairs. *Schroeteria* was merged with *Schizonella* by Thirumalachar & Whitehead (1968), an unfortunate solution. Nagler, Bauer, Berbee, Vánky & Oberwinkler (1989) studied the germination and ultrastructure of *S. delastrina* and *S. poeltii* and demonstrated that they are Ascomycota. *Type of the genus:*

Schroeteria delastrina (Tul. & C. Tul.) G. Winter,

in Rabenhorst, Kryptogamen-Flora, etc., 2. Aufl., 1. Pilze, I. Abt.: 117, 1881.

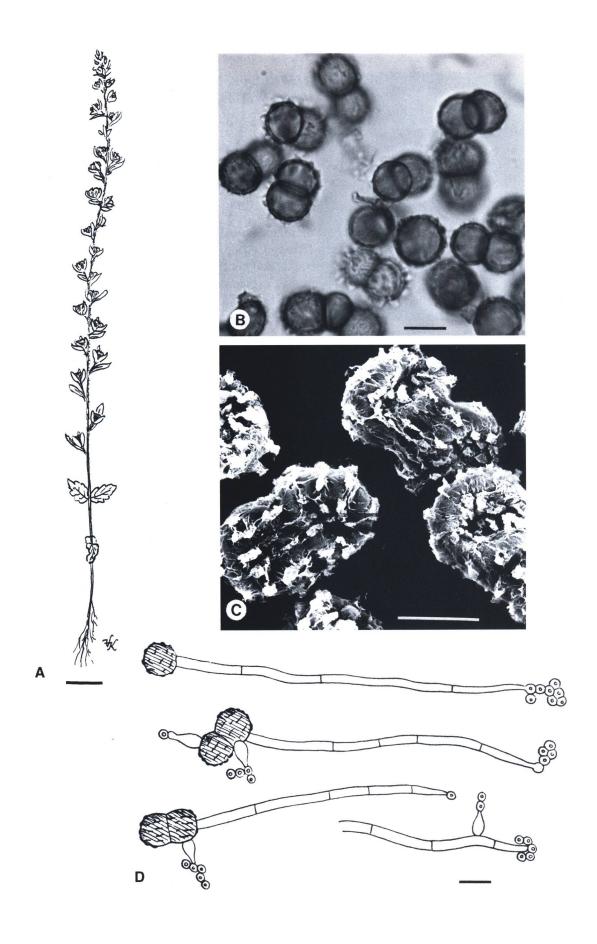
Thecaphora delastrina Tul. & C. Tulasne, Ann. Sci. Nat. Bot., Sér. 3, 7:108, 1847. — Geminella delastrina (Tul. & C. Tul.) J. Schröter, Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss. 1869/1872:5, 1869, Hedwigia 9:137, 1870. — Schizonella delastrina (Tul. & C. Tul.) Thirumalachar & Whitehead, Amer. J. Bot. 55:186, 1968. — Type on Veronica praecox, France, Dépt. Vienne, Poitiers ("Pictavia"), leg. Ch. J.L. Delastre.

Sori (Fig. 104 A) in seeds destroying them completely and filling the capsules with a grayish brown, powdery spore mass. Spores (Figs. 104 B, C) usually in pairs, sometimes in threes or single, globose, subglobose to irregular, flattened on the contact sides, 8-11(-13) x 8-11(-13.5) μm, pale olivaceous brown; wall 0.5-1 μm thick, coarsely verruculose and ribbed, verrucae usually arranged in 1-2 µm high rows or long ridges, running more or less parallel with the long axis of the formed sporogenous hyphae. Spore germination (Fig. 104 D) results in a long, septate germ tube, sometimes with short, lateral branches, but also in a short, aseptate, bottle-shaped germ tube. On the top of each germ tube, or branch of germ tube, successively 2-12, globose, hyaline conidia diameter produced, often chains ("sporidia") measuring 3 um in are 1981a:164-165). Septal pore simple, with pore plug and Woronin bodies at the septa (see fig 7, p. 20).

On Scrophulariaceae: Veronica acinifolia L., V. agrestis L., V. arvensis L., V. praecox All., V. triphyllos L., V. verna L.; cosmopolitan.

Ref.: Liro 1938, Thirumalachar & Whitehead 1968, Vánky 1981a, 1983, Nagler, Bauer, Berbee, Vánky & Oberwinkler 1989.

- Fig. 104 A-D. Schroeteria delastrina on Veronica arvensis, Vánky, Ust. exs. no. 9, HUV 1615.
- A. Sori in seeds of an apparently healthy plant. Habit (Bar = 1 cm).
- **B, C.** Spores in LM and in SEM (Bars = $10 \mu m$).
- **D.** Spore germination (after Vánky 1981a; Bar = $10 \mu m$).



DOUBTFUL GENERA

(105). CROZALSIELLA R. Maire,

Bull. Soc. Hist. Nat. Afrique N. 8:144, 15.VII.1917.

The original description of this genus is as follows:

Sori first hard later pulverulent, formed in the inner parts of the host, lacking columella. Spores formed successively, centripetally from the periphery of the lacunae of the culms. It differs from Cintractia by centripetal, not centrifugal mode of spore formation, and by absence of columella; from Sphacelotheca by the fertile pseudo-membranous stroma.

Crozalsiella is a unispecific genus. It seems that there are no sufficient reasons to maintain it as a separate genus. It belongs to the heterogeneous Sporisorium-Ustilago group. It was considered a synonym of Ustilago (Vánky 1985b:11) but further analyses by modern methods and comparison with other similar smuts are needed to find out its correct generic position. A second species, C. argentina Hirschhorn (1940:236), type on Panicum demissum Trin., Argentina, is a Sporisorium (det. K. Vánky). Type of the genus: Crozalsiella aeluropodis (Trotter) R. Maire (= Ustilago aeluropodis).

Crozalsiella aeluropodis (Trotter) R. Maire,

Bull. Soc. Hist. Nat. Afrique N. 8:144, 1917.

Sphacelotheca aeluropodis Trotter, in Saccardo & Trotter, Ann. Mycol. 11:413, 1913 (as "aeluropi"). -- Ustilago aeluropodis (A. Trotter) K. Vánky, Publ. Herb. Ustilag. Vánky (HUV) 1:11, 1985b. -- Type on Aeluropus repens (= A. lagopoides), Tripolitania [= Libya], Misurata, Bu Sceifa, in "sebkha", 15.IV.1913, leg. A. Trotter.

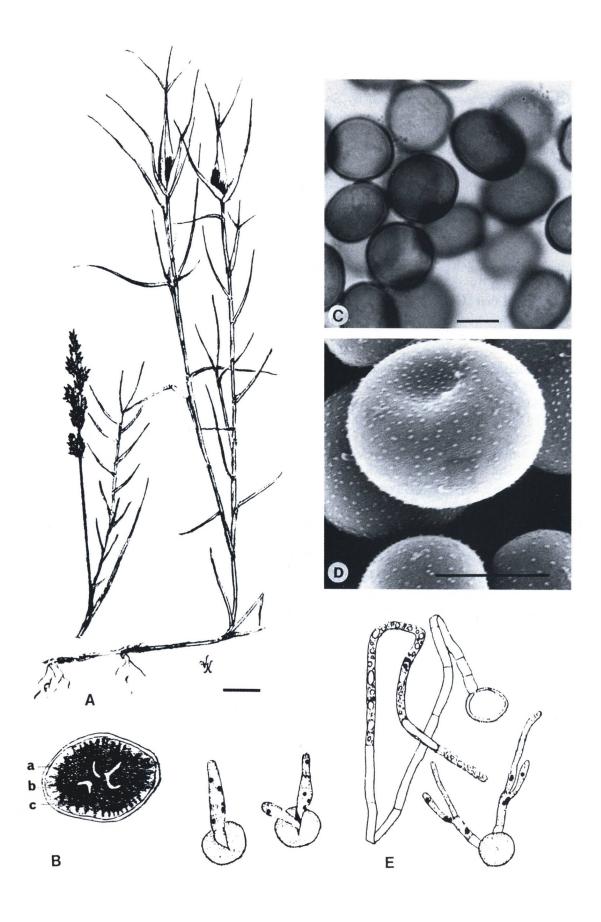
Sori (Figs. 105 A, B) on the tip of culms replacing the inflorescence, ovoid or fusiform, 1-2 cm long, invested by a rosette of leaf-sheaths and young leaves, later rupturing laterally to expose the dark brown, powdery spore mass. *Spores* (Figs. 105 C, D) varying in shape and size, globose, subellipsoidal or ellipsoidal, often slightly flattened, 12-17 x 13.5-20 μm, golden-brown; wall uniform, 0.5-1 μm thick, in LM sparsely to moderately densely, minutely punctate-verruculose; the verrucae do not or only slightly affect the spore profile; in SEM minutely verruculose-echinulate. Peridium, sterile cells and columellae are lacking. *Spore germination* (Fig. 105 E) results in septate basidia and hyphae (Maire 1917:143).

On Poaceae: Aeluropus laevis Trin., A. lagopoides (L.) Trin. ex Thwaites (A. repens (Desf.) Parl.; A. villosus Trin.), A. littoralis (Gouan) Parl.; Europe, Africa, Asia.

According to Maire (1917) the spores are produced centripetally, with oldest spores in the middle of the sori and the youngest ones toward the periphery.

Ref.: Saccardo & Trotter 1913, Maire 1917, Zambettakis 1968.

- Fig. 105 A-E. Crozalsiella aeluropodis on Aeluropus littoralis. A, C, D. Vánky, Ust. exs. no. 481 (as Ustilago aeluropodis), HUV 11545. B, E. after Maire (1917:143).
- A. Sori in two inflorescences of a plant, and a healthy inflorescence. Habit (Bar = 1 cm).
- **B.** T.S. of a sorus. (a) = host tissue, (b) = mycelial stroma, (c) = spore mass.
- C, D. Spores in LM and in SEM (Bars = $10 \mu m$).
- E. Spore germination (after Maire 1917:143, figs G, D, H).



(106). ENDOTHLASPIS N.V. Sorokin,

Rev. Myc. (Toulouse) 12:4, 1890.

The genus *Endothlaspis* was introduced by Sorokin to accommodate two smuts: *E. melicae* Sorokin on *Melica ciliata* L., and *E. sorghi* Sorokin on *Sorghum cernuum* (Ard.) Host (= *S. bicolor* (L.) Moench, syn. *S. vulgare* Pers.), both from Central Asia. Langdon & Fullerton (1978:448) analyzed this genus and stated that "*Endothlaspis* is poorly defined and its status is obscure".

Sorokin's characterization of this genus may be summarized as follows: "The filaments of mycelium destroy the ovaries" and there is a fungal pseudoperidium around each "spore mass" [= sorus]. Furthermore, Sorokin emphasized the lack of a columella. This statement, however, may be incorrect; Sorokin's pictures showing numerous filiform columellae.

Most authors considered *Endothlaspis* to be a synonym of *Sphacelotheca* (G.P. Clinton 1904, Ciferri 1928, Ainsworth & Sampson 1950, Zundel 1953, Fischer 1953, Fischer & Holton 1957). Langdon & Fullerton (1978:448) concluded that "Until more evidence is available there is no justification for regarding *Endothlaspis* as a synonym of *Sphacelotheca*". However it is now established that *Sphacelotheca* is restricted to host plants in the Polygonaceae only.

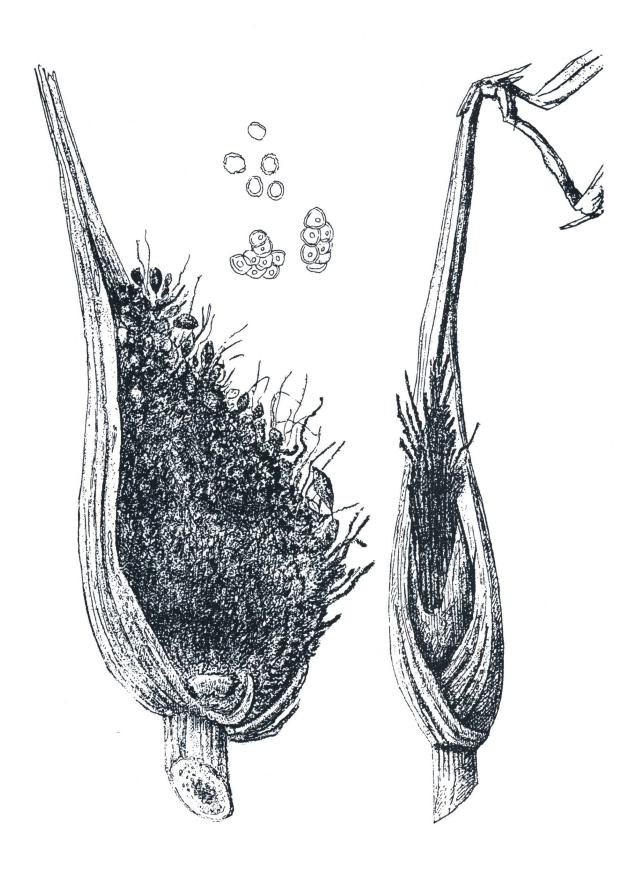
Concerning *Endothlaspis melicae*, Langdon & Fullerton (1978) stated: "Sorokin's specimens have not been located nor have we found any record of a smut of *Melica* which might possibly be conspecific with *Endothlaspis melicae*.... Sorokin's data are difficult to interpret.... The characters of *Endothlaspis melicae* remain obscure". On the other hand, it is possible that the host plant was wrongly identified by Sorokin.

Regarding *Endothlaspis sorghi*, Sorokin described it as possessing echinulate spores of 7-10 μm in diameter. He insisted that the smut he described was not the same as *Ustilago reiliana* (= *Sporisorium reilianum* (Kühn) Langdon & Full.). This last species destroys the whole inflorescence and has larger spores (10-14.5 μm). However, there are three other smuts on *Sorghum* which may be taken into consideration, all forming sori in the florets, with a dark brown, dusty spore mass. These are: *Sporisorium sorghi* Ehrenb. ex Link, *S. cruentum* (Kühn) Vánky, and the rare *Ustilago bulgarica* Bubák. The first produces no or only little congestion of the inflorescence, the sori have a thick peridium, and the spores measure 5.5-8.5 μm in diameter. *S. cruentum* produces markedly congested panicles, the sorus has a thin peridium and the spores are 6.5-10 μm in diameter. *Ustilago bulgarica* has short corniculate, irregularly bullate sori with a polycystic structure, covered by a thin membrane, and spores very finely punctate, 5-8(-9) μm in diameter.

An analysis of Sorokin's description and illustration of *Endothlaspis sorghi*, and a comparison with these three species, shows with great probability, that it is identical with *Sporisorium cruentum*, which means that *Endothlaspis* is a synonym of *Sporisorium*.

Ref.: Sorokin 1890, Langdon & Fullerton 1978.

Fig. 106 *Endothlaspis sorghi* on *Sorghum bicolor* (L.) Moench (after Sorokin 1890, Pl. XXI). Two diseased inflorescences with the sori, spores (top middle) and two groups of sterile cells.



(107). *JULIOHIRSCHHORNIA* Hirschhorn (as *Juliohirschhorni*), *Las Ustilaginales de la flora Argentina*:93 & 529, 1986.

This genus was proposed on the basis of spore germination, which is "intermediary between the Ustilaginaceae and Tilletiaceae" (Hirschhorn 1959:315). It was characterized as follows: *Sori* destroying the whole inflorescence, 2-7 cm long, 3-4 mm wide, first covered by a thin, brownish membrane which ruptures irregularly disclosing the blackish brown, powdery spore masses. *Spores* globose, ellipsoidal or pyriform, golden-brown or yellowish, with germ pores. Promycelia (basidia) septate on which sporidia (basidiospores) and also branches are formed. On the top of the branches, on 2-5 sterigmata, globose or ovoid sporidia are produced. Sporidia are provided with apical appendix on which new, similar spores are produced. *Type of the genus:*

Juliohirschhornia linderi (E. Hirschhorn) E. Hirschhorn (as "*Juliohirschhrni*"), *Las Ustilaginales de la flora Argentina*:530, 1986 (comb. illeg.).

Ustilago linderi Hirschhorn, in Omagiu lui T. Săvulescu:311, 1959. Invalidly published, no type indicated (ICBN 37.1). — On Paspalum notatum Flüggé, "P. paludivagum" (=? Paspalidium paludivagum (Hitchc. & Chase) Parodi), P. plicatulum Michaux, P. vaginatum Swartz, Paspalum sp., Argentina, Salta Prov., near San Lorenzo, leg. E. Hirschhorn.

Sori (Fig. 107 A) destroying the whole inflorescence, 0.3-0.4 x 2-7 cm, first covered by a thin, brownish membrane which ruptures irregularly disclosing the blackish brown, powdery spore masses. Spores (Figs. 107 B, C) globose, subglobose, ovoid, pyriform, irregular, or ellipsoidal with bilateral elongation, 6-14 x 7-10 μm, golden-brown or yellowish; wall thin, punctate, minutely verruculose or echinulate, rarely smooth. Spore germination (Fig. 107 D) results in 4-celled basidia on which basidiospores and also branches are formed. On the top of the branches, on 2-5 sterigmata, globose or ovoid sporidia are produced. Sporidia with apical appendix on which new, similar spores are produced. Spores often germinate also with ramified mycelia, without production of sporidia.

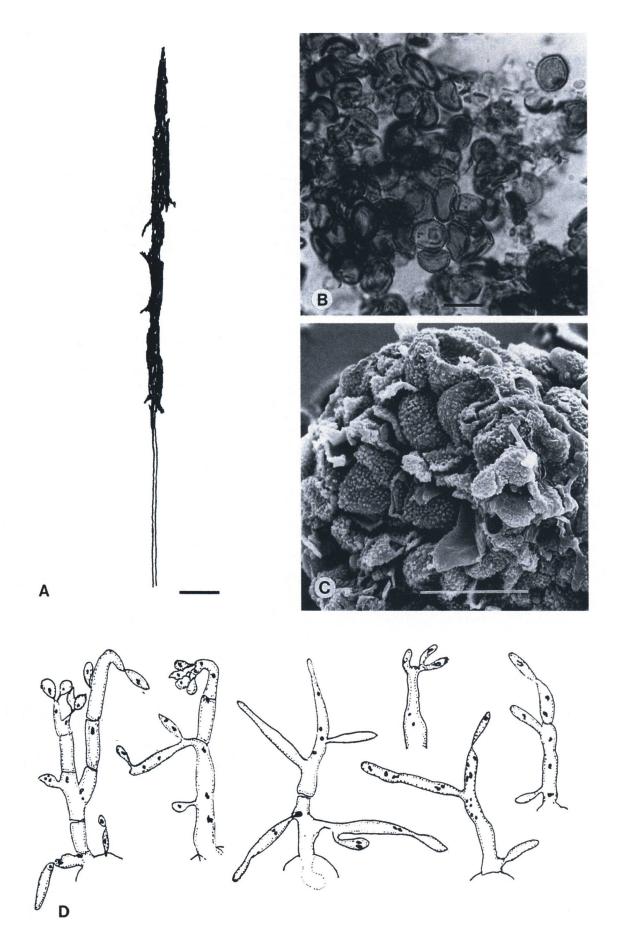
On Poaceae: Paspalum notatum Flüggé, "P. paludivagum" (=? Paspalidium paludivagum (Hitchc. & Chase) Parodi), P. plicatulum Michaux, P. vaginatum Swartz, and Paspalum sp.; S America (Argentina, Uruguay).

Apart from the fact, that the genus is invalid, based on an invalidly published species, the type of spore germination seems to represent only a variant of the *Ustilago*-type and not an intermediate form between *Ustilago* and *Tilletia*. Other characters are also identical with those of numerous species of *Ustilago* or *Sporisorium*. According to Elisa Hirschhorn (in litt.), the type of this species no longer exists. Indeed, the minute fragment of the "type" of *J. linderi* on *Paspalum plicatulum* Michaux (Argentina, Salta Prov., near San Lorenzo, II.1942, E. Hirschhorn), in Herb. Hirschhorn no. 1005 (Instituto Fitotecnico de Santa Catalina, Llavallol, Buenos Aires, Argentina), is completely destroyed by insects. It is improper to designate it as a lectotype. Study of this smut on freshly collected specimens is desired to elucidate its generic position.

Ref.: Hirschhorn 1959, 1986.

Fig. 107 A-D. Juliohirschhornia linderi on Paspalum notatum and P. plicatulum, "Type".

- A. A sorus destroying the whole inflorescence. Habit (after Hirschhorn 1959:303).
- **B, C.** Spores in LM and in SEM from *P. plicatulum* (destroyed by insects; Bars = $10 \mu m$).
- **D.** Spore germination (on WA, at 25 °C, in 1-2 days; after Hirschhorn 1959:314).



REGIONAL FLORAS

Africa (Zambettakis 1971; K. & C, Vánky & Denchev 2011), Argentina (Hirschhorn 1986), Australia (McAlpine 1910; Vánky & Shivas 2008), Azerbajdzhan (Uljanishchev 1952, 1959), Baltic Region (Ignatavičiūtė 1975), Brazil (Viégas 1944), Bulgaria (Denchev 2001), Carpathian Region, mainly Hungary (Hazslinszky 1877; Moesz 1950; Vánky 1985a), China (Ling 1953; Wang 1963, 1964; Guo 2000, 2011), Colombia (Molina-Valero 1980, Piepenbring, 2002), Costa Rica (Piepenbring 1996), Cuba (Piepenbring & Hernández 1998), Czech Rep. (Bubák 1912, 1916), Denmark (Rostrup 1890), Ethiopia and Eritrea (Vánky 2005d), Europe (Vánky 1994), Finland (Liro 1924, 1938), France (Viennot-Bourgin 1956), Germany (Lindau 1912; Hirsch & Braun 1980; H. & I. Scholz 1988, 2000), Great Britain (Plowright 1889; Ainsworth & Sampson 1950; Mordue & Ainsworth 1984), Hungary (Vánky, Gönczöl, & Tóth 1983('1982'); see also Carpathian Region), India (Mundkur & Thirumalachar 1952; Gandhe 2011), Indian Subcontinent (Vánky 2007b), Iran (Ershad 2001; Vánky & Abbassi 2013), Israel (Savchenko, Heluta, Wasser, Nevo 2011('2010')), Italy (Ciferri 1938), Japan (Ito 1936; Kakishima 1982), Kazakhstan (Schwarzman 1960), Lithuania (Ignatavičiūtė 2001), Mexico (Durán 1987), Neotropical countries (Piepenbring 2003), New Zealand (Cunningham 1924, 1945b; Vánky & McKenzie 2002b), North America (Clinton 1902, 1904, 1906; Zundel 1939b; Fischer 1953), Norway (Jørstad 1963), Pakistan (Ahmad 1956), Poland (Kawecka-Starmachowa 1935, 1939; Kochman 1936; Kochman & Majewski 1973), Romania (Săvulescu 1957b), Russian Far East (Azbukina, Karatygin & Govorova 1995), South Africa (Zundel 1938), Soviet Union [Russia] (Gutner 1941; Karatygin & Azbukina 1989; Azbukina & Karatygin 1995), Sweden (Lindeberg 1959), Switzerland (Schellenberg 1911; Zogg 1986('1985')), Ukraine (Savchenko & Heluta 2012) Uzbekistan (Ramazanova, Ahmedova, Sagdullaeva, Kirgizbaeva & Gaponenko 1987), Yugoslavia (Lindtner 1950).

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